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A re-evaluation of crinoid morphology and proposed relationship of crown groups, with insights from biogeography

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A re-evaluation of crinoid morphology and proposed relationship of crown groups, with insights from biogeography

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Abstract

A re-evaluation of crinoid morphology and proposed relationship of crown groups, with insights from biogeography

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Crinoids are the most primitive living members of the Phylum Echinodermata. Though still present in reduced numbers today, crinoids were the dominant echinoderms from the Ordovician to the Permian. The crinoid body plan consists of three major regions, the column, the calyx, and the arms. Each region serves important functions in crinoids. The column raises the rest of the body into the water column for more efficient feeding. The calyx contains the visceral mass and mouth. Arms extend out from the top of the calyx to trap microorgansisms and suspended organic particles in the water column. A re-evaluation of these functional units is undertaken to understand the importance of various structures and to obtain discrete characters for use in a cladistic analysis.

The relationship of crinoid crown groups has been an active area of research for the past couple of decades. With each proposed phylogenetic relationship, a new interpretation of thecal plate homology has been proposed.

Here each study is re-examined in the light of new data. A review of functional morphology indicates a dual-reference system to be the most supported interpretation of plate homology. The two reference points in this system are the stem-cup and the cup-arm junctions, at the top and bottom of the calyx. The difference between a two-circlet and three-circlet crinoid is the presence or absence of the middle (basal) circlet. A new cladistic analysis is presented, with the topology of trees obtained giving support for the retention of Paleozoic crinoid stem and crown groups.

Crinoids appear abruptly in the fossil record. Questions pertaining to origins and ancestral stock abound. A biogeography study is employed to look at the distribution of crinoids from the Early to Middle Ordovician. Locality information, combined with an understanding of the movement of major plates, paleoclimate data, an understanding of larval distribution, and a review of similar studies carried out on different taxa, gives insight into possible radiation and dispersal patterns of crinoids from the first half of the Ordovician.

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Chapter 1: *Functional Morphology of Paleozoic Crinoids*

INTRODUCTION

The purpose of this chapter is to understand morphology and function of crinoids. Ultimately the goal is to understand how function and morphology are affected by evolutionary forces in the early life-history of crinoids. In order to understand the function of structures in fossil crinoids it is important to review basic living crinoid morphology. Crinoids are generally passive suspension feeders, relying on ocean currents to bring in nutrients. Though typically attached to substrate, crinoids will orient themselves in a way that allows for efficient feeding. After fanning out the arms, modern crinoids use their longest tube feet to collect particles, and intermediate tube feet to deposit them into food grooves on the oral side of the arms. The shortest tube feet within the food groove move the particles to the oral surface and eventually to the mouth. To understand the functional morphology of crinoids, the skeleton can be divided into major functional units: the column, the calyx, and the arms (Figure 1.1). Evaluating function within and between these units can help discern what structures are functionally significant.

ECHINODERM MORPHOLOGY

Crinoids are members of the Phylum Echinodermata, and are differentiated from most marine invertebrates by being deuterostomes. At least four phyla (of approximately 32) are members of Deuterostomia; included with Echinodermata are the Chordata, Hemichordata, and Xenoturbellida. Deuterostomes differ from the other major group of animals, the proterostomes, by the blastopore becoming the anus rather than the mouth. Deuterostomes also

show a radial cleavage pattern as opposed to a spiral pattern. Most representatives of the deuterostomia are further characterized by an internal skeleton, a poorly centralized nervous system and no cephalization.

Echinoderms are united by the presence of a complex series of fluid-filled canals called the water-vascular system (WVS), which is an extension of the internal coelom. Though bilaterally symmetrical in the larval stages, most adults of this phylum exhibit some degree of pentameral symmetry superimposed over a bilateral system. They possess an endoskeleton composed of calcium carbonate plates with a porous internal fabric called stereom, and have mechanically active collagenous connective tissue between the plates. Adult echinoderms also lack a true heart and brain, and have the unique ability to autotomize body parts when attacked.

Anatomical terms applied to bilateral organisms cannot be easily applied to those with pentameral symmetry. Recent studies have attempted to apply anterior/posterior terms to echinoderms (Mooi & David, 2008) based on developmental order of coelomic sacs, but application of these terms can be confusing to those not familiar with echinoderm development, or those familiar with the term in a bilaterian sense. Anatomical references in echinoderms are generally referred to by relation with the mouth. Body surfaces are designated oral (near or towards the mouth) or aboral (far from or away from the mouth). Motile echinoderms are oriented with the oral surface down, whereas taxa bearing a stem and fixed in position are oriented with the oral surface up (likely a primitive orientation). The skeleton of an echinoderm can be divided into two parts based on construction, the ambulacral and interambulacral areas. Ambulacral areas are those with pores through which structures called tube-feet

(or podia) extend, and these areas are intimately related to the radial canals of the water-vascular system. Interambulacral areas are those in between the ambulacral areas and lack podial pores, although they may have openings of other kinds.

The WVS is a unique and important structure in echinoderms. This system generates, distributes, and controls hydrostatic pressure necessary to control the tube feet. The WVS secondarily functions as a medium for gas exchange and removal of waste in living echinoderms (Nichols, 1972). The WVS is comprised of a series of fluid-filled canals derived during embryonic development (Figure 1.2). The fluid is primarily composed of sea-water, though it contains a dense population of coelomocytes in suspension. Coelomocytes are thought to function as part of the immune system of echinoderms (Nichols, 1972).

Water enters the system at the hydropore. The hydropore can be covered by a small, sieve-like plate called a madreporite in some taxa, although in many crinoids it has been shown to open directly into the coelom (Nichols, 1966). A canal called the stone canal connects the hydropore to the ring canal, a structure wrapping around the esophagus in most extant taxa. From the ring canal, five symmetrically oriented radial canals extend out the rays. Tube feet branch off the radial canals.

Tube feet (or podia) serve a variety of functions in crinoids. In modern taxa the tube feet are utilized for locomotion, feeding, and respiration. Diffusion of oxygen through the thin membrane covering the tube-feet likely fulfills the oxygen requirement of crinoids. This is supported by the presence of cilia on the

internal surface of each podium to help facilitate fluid movement (Pechenik, 2000, p. 480).

Echinoderms show a reduced oxygen consumption rate when compared to other invertebrates of the same mass. Observations of the holothurian *Actinophya muritiana* show an oxygen consumption of about 0.48 ml/hr, whereas a "standard" invertebrate of the same mass showed an oxygen consumption of 11.9 ml/hr (Nobuhiro, 2009). Similarly, echinoderms tend to show lower energy consumption when compared with other animals of the same mass (Lawrence & Lane 1982). This is attributed to the presence of a large amount of calcite in most taxa and a lack of muscular development, along with a generally sluggish pace of movement. Also present is mechanically active collagenous connective tissue. The presence of a robust calcite test gives structural support while requiring no energy. Mechanically active connective tissue, unique to echinoderms, can change its mechanical properties through non-muscular mechanisms. Essentially, the tissue can become rigid or flaccid when necessary. Therefore, once a crinoid is in feeding position under stable currents, the tissue can become rigid, requiring little to no energy expenditure.

CRINOID MORPHOLOGY & FUNCTION

Crinoids were the dominant echinoderm clade for the entire post-Cambrian Paleozoic Era. Many modern crinoids are highly derived, losing all but one circlet in the aboral cup, and abandoning an attached lifestyle in favor of mobility. Given the focus of my studies is Early Paleozoic crinoids, morphology here will relate to those clades dominant in the Paleozoic.

Paleozoic stemmed crinoids are commonly attached to the substrate by a variety of different holdfasts, depending on the composition of that substrate. The holdfast attaches to a series of calcite discs called columnals. These discs are stacked to form the column, often referred to as a stem. In certain taxa, small appendages called cirri (sing. cirrus) project from the column. Atop the column is the calyx. The calyx is a cup-shaped structure that contains the digestive system, viscera, and mouth. The oral surface of the calyx is covered by a tegmen, a plated membrane bearing the mouth. Arms project upwards from the edge of the calyx. Primitively these arms were atomous (unbranched) or isotomous (branching equally to each side). Paleozioc taxa have been discovered bearing 5, 10, 20, 40, or even as many as 200 arms. The five rays extending from the radial plates in crinoids are designated A, B, C, D, and E. Ray A (anterior) is defined as opposite the interray containing the anal structure (considered posterior). A clockwise sequence from ray A gives each ray the proper designation (Figure 1.3) (Ubaghs, 1978a).

COLUMN

The column is important for elevating the other regions up into the water column and orienting the organism properly in the current. The crinoid stem can be divided into two distinctive components; an attachment structure and the elevating column. The attachment structure, the holdfast, anchors the organism to substrate. Anchoring is necessary to allow stabilization and changing of position while suspension feeding. Attachment structures are varied, including; (1) direct cementation to hard substrate, (2) branched in all directions, similar to a tree root, (3) coiled around a supporting structure, or (4) recumbent, with a

number of rooting points (Brett, 1981). Different anchoring strategies likely correspond to substrate composition and differing wave energy. Holdfasts are commonly discovered attached to sea-floor beds, though the stem and calyx has often become disarticulated making classification of holdfasts difficult.

During the Cambrian and Ordovician, much of the diversity of marine life was composed of sessile suspension feeders. The ability to move higher in the water column would allow organisms to reach new food sources and occupy new niches. By the Late Ordovician some taxa had developed columns 60 to 100 centimeters in length (Lane, 1963). Most crinoids in the Paleozoic possessed columns not exceeding 1.25 meters (Ausich and Bottjer, 1982), and many were less than ten centimeters in length.

The composition of columnals varies among crinoids. Although most crinoids possess circular, one-piece columnals (holomeric construction), many taxa in the Early and Middle Ordovician have columnals composed of a number of separate pieces, termed meres. Meric stems are common early in the history of crinoids. Through time theses eventually become uniform in orientation, and finally fuse into holomeres (Fig 3B-G). When meres are present they are roughly organized into columnals. Typically the meric columnals are composed of five plates, termed pentameric (Figure 1.4A). However, some Ordovician taxa are tri- or tetrameric in construction (Donovan, 1986). Forming in the center of the columnals is an axial canal. In recent crinoids, this canal contains coelomic and nervous extensions from each of the five lobes of the chambered organ, and likely held the same function in Paleozoic taxa (Ubaghs, 1978a).

Serially arranged columnals form the column. An articulation facet is present between two consecutive columnals. These facets are of three main

types. Synostosis articulations (Figure 1.5A) are facets that are planar, with inflexible joints between plates. This type of articulation is common in taxa from the Ordovician. Symplexic articulations (Figure 1.5B) are present in most taxa. Their diagnostic feature is the presence of crenularia, which are ridges radiating out from the center of a columnal. Crenularia from adjacent columnals interlock, and help to prevent the column from over-rotating while erect in the water current. This pattern of radiating ridges also allows for flexibility in 360 degrees (Donovan, 1989). The third type of articulation is synarthy (Figure 1.5C). This form is the most flexible, with each column coming into contact with another's fulcral ridge. Each type of articulation lacks musculature (Donovan, 1989). As the area of contact between columnals increases, there is increased strength at the cost of flexibility. Eventual fusion of mere circlets resulted in holomeric columnals (Donovan, 1999).

During growth, individual columnals are introduced at the proximal end of the column (stem-cup junction). In taxa possessing homeomorphic columnals, all columnals have a uniform diameter, and each columnal is added in turn. Taxa with heteromorphic stems, those with columnals varying in diameter, are composed of nodals (larger diameter columnals) and internodals (smaller diameter columnals). During growth, the nodals are added at the proximal part of the stem, whereas internodals are added between two nodals at short but different distances from the cup (Ubaghs, 1978a; Guensburg, 1992). A third type of stem, xenomorphic, is seen in some taxa. These columns show differing morphology in different parts of the stem. This type of stem often possesses three distinct areas: the proxistele, mesistele, and dististele. The variation in stem structure over its length has been attributed to ontogenetic development,

because the dististele is earliest formed and the proxistele is last-formed. (Ubaghs, 1978a)

STEM-CUP JUNCTION

The column contacts the crown at the stem-cup junction. An important relation is seen in most taxa at this juncture, referred to as the "Law of Wachsmuth and Springer". According to the rule, in dicyclic crinoids (crinoids with three plate circlets in the aboral cup) the columnal pentameres and the outer angles of the stem are directed interradially and therefore alternate with infrabasals, whereas the sides of the stem are located perradially (Figure 1.6A). In contrast, monocyclic crinoids (crnoids with three plate circlets in the aboral cup) have the columnal pentameres and outer angles of the stem perradial while longitudinal sutures are interradial (Figure 1.6B) (Ubaghs, 1978a). Although this law is effective for understanding the stem-cup junction in most crinoids, some early taxa such as *Aethocrinus moorei* have a circlet below the infrabasals that does not show the 36 degree rotation expected by the law (Figure 1.7). Various authors have tried to resolve this issue (Ubaghs, 1968, 1972; Philip and Strimple, 1971; Warn and Strimple, 1977; Ausich, 1996; Guensburg & Sprinkle, 2003), with alternate interpretations resulting in differing classifications of this taxon.

CALYX

The aboral cup is the part of a fossil crinoid most commonly used for identification and classification of this group (Ubaghs, 1978a). It is an area of conflict among researchers with regards to homology (Simms, 1994; Ausich, 1996; Rozhnov, 2002; Guensburg & Sprinkle, 2003). However, this area does contain the visceral mass and in some unique taxa from the Paleozoic, pore

structures are present. These pore structures are interpreted as areas for gas exchange. The aboral cup typically takes one of two main forms. The aboral cup is composed of two (monocyclic) or three (dicyclic) circlets of five polygonal plates (Figure 1.8). This creates the 'ideal' form, though modification has been seen in some taxa. Reduction of infrabasal plates had produced taxa with three, or even a single plate present in this circlet. The radial circlet is interrupted by an anal series in certain taxa, and many camerate crinoids have brachial plates and interradials incorporated into the calyx.

The interruption of plating in the radial circlet occurs differently among the several groups of Paleozoic crinoids. Some authors have argued that the anal series of different clades are homologous (see Simms, 1994), although others have considered the structures to be analogous (Ubaghs, 1978a; Rozhnov 2002).

Crinoids belonging to the camerate clade have an anal structure composed of a small anal pyramid elevated above the calyx in the tegmen (Figure 1.9). The radial circlet is often interrupted at the CD-interray, producing a wider posterior side. The primanal plate is present either between or slightly elevated with respect to the radial plates. The location of the primanal with respect to the radial circlet is considered to be very important taxonomically (Ubaghs, 1978b). Here we must note that the primanal of camerate is thought to be morphologically different than the radianals seen in other taxa (Ubaghs, 1978b).

Taxa belonging to the disparid clade possess an arm-like process with an anal structure present at the distal terminus (Figure 1.10). This structure has been interpreted as a morphological combination of the rectum with the left

branch of the C-ray arm (Rozhnov, 2002). Disparids possess all anal plates outside the cup. An elongation of the anal structure into a cylindrical tube or elongated sac is common, leading to differing hypotheses about its function in life. The structure could house gonads, play a role in respiration, or possibly increase the overall length of the digestive system (Rozhnov, 2002).

Taxa in the cladid clade possess an anal structure represented by a large anal sac, covered with plates. This structure occupies a large space in the CD interray of the calyx (Figure 1.11). This type of structure differs from that of disparids based on size, proximal inclusion into the calyx, and the presence of an anal X plate. Typically 1-2 anal plates are incorporated into the calyx.

Although the disparid and cladid clades differ in arrangement of the anal series, morphological series studies have shown some possible homology between the structures. The radianal plate of cladids is hypothesized to be homologous to the C-radial in the disparid stock. The anal X is interpreted as being homologous to the first plate of the anal tube in disparids (Rozhnov, 2002).

CUP-ARM JUNCTION

The point of union between the arms and the cup occurs on the radial plates. Previous authors have suggested arms may originate on plates other than radials (Simms 1994, Ausich 1996), but if different groups of crinoids originated from a single ancestor bearing arms, the union between arms and cup should be an important functional site. The site of articulation between the first primibrachial and the radial plate is called the radial facet. These facets can be described as angustary (the width is narrower than the distal margin of the arm-bearing plate), peneplenary (almost as wide as the distal margin of the arm-

bearing plate), or plenary (narrower than the distal margin on the arm bearing plate).

Traditionally the radial plates of some taxa were interpreted as being transversely divided into two parts. It was reasoned that the two plates together function as a single brachial plate. Based on serial homology, supposed superradials are likely fixed brachials, as seen in the protocrinid stock (Guensburg and Sprinkle 2003).

In some primitive taxa, as well as most members of the camerate stock, multiple extra plates are incorporated into the calyx. The inclusion of fixed brachials, fixed pinnules, and interbrachial plates in the calyx has been proposed as a specialization (Ubaghs, 1978a). However, recently discovered taxa from the Early Ordovician (*Titanocrinus, Alphacrinus)* are currently regarded as belonging to different clades, but show brachials incorporated into the calyx. Multiple plates included above the radial plates is therefore more likely a plesiomorphic characteristic rather than a specialization as previously hypothesized.

ARMS

The arms comprise the feeding net and the terminus of the water-vascular system. Crinoids are passive suspension feeders, relying on external currents for food supply. The arms of crinoids are jointed feeding appendages that arise from radial plates, the uppermost circlet of plates in the aboral cup. Arm branching can be described as atomous (Figure 1.12A), isotomous (Figure 1.12B), or heterotomous (Figure 1.12C). Primitive crinoids mostly possess arms showing an isotomous branching pattern. Branching of arms greatly increases the filtering net cast, and therefore can help increase feeding efficiency. The arm

rays of crinoids are composed of a series of individual plates called brachials. Branching of the arms occurs on specialized brachials called axillaries. Brachial plates are designated by the distance from the radial plate and by how many times the arm has bifurcated before the plate in question formed. For example, the first plate originating on the radial would be referred to as primibrach 1; a brachial plate present immediately above the first axillary is termed secundibrach 1, and so on.

Two major classes of articulations are seen between the brachial plates, ligamentary or muscular. Ligamentary articulations have ligaments that are involved in joining brachials. Muscular articulations possess a combination of muscle and ligament fibers. The types of articulations seen in Paleozoic crinoids are reflected in the microstructure of the calcite plates. Ligament fields are identifiable by a coarse pore structure that allows for deep penetration of ligament fibers. Muscle fields, in contrast, are fine meshed because the muscle tissue does not need to penetrate deeply into the stereom (Ubaghs, 1978a). Muscles in this instance do possess contracting power, and muscular arms in modern comatulids allow for a mode of swimming (Brower, 17973). Muscular articulations in the Paleozoic are judged to have existed only within the cladid and disparid clades (Van Sant and Lane, 1964). Much of what is postulated about articulation in Paleozoic crinoids has been inferred from post-Paleozoic stock. Ligaments help the arm rays of a crinoid extend out into a feeding position. It is likely that the ligament composition of crinoids differs from ligaments seen in other phyla. What would happen if ligaments behaved like those seen in bivalves, which force the valves to separate after death? Arms would be forced to splay out and would be much more likely to become

disarticulated after death (Van Sant and Lane, 1964). Based on numerous fossil examples this is not the case. The idea that ligaments present in the crinoid have some degree of movement is supported by articulations within the column and cirri. It has been shown that articulations in the column and cirri are composed entirely of ligaments (Donovan, 1989), but still have an ability to move the crown of the organism in the water column.

Two types of muscular articulation can be observed in crinoids. Both straight muscular articulations (Figure 1.13A) and oblique muscular (Figure 1.13B) articulations have a similar basic morphology. The surface of a brachial plate possesses a transverse ridge extending from one lateral edge to another. Five fossae are present on the surface of a brachial plate as well. The two types of muscular articulation differ in the orientation of the transverse ridge with respect to the aboral-oral axis. Straight muscular articulations present a transverse ridge perpendicular to the aboral-oral axis, creating symmetrical right and left halves. Oblique muscular articulations possess a transverse ridge that meets the aboral-oral axis at an angle, resulting in asymmetrical halves (Ubaghs, 1978a). The structure of an oblique muscular articulation produces, in aboral view, a variation in height of the lateral sides of a brachial. Alternating sides with each plate, the side presenting the high lateral side often possesses a socket for pinnule attachment.

Ligamentary articulations can be described as movable or immovable. Movable articulations allow a certain amount of differential movement between plates. Immovable articulations allow only slight movement or no movement at all.

Movable articulations come in a variety of forms, with many intermediates present. However, three major types of articulation are pertinent to this. Trifacial articulations (Figure 1.14A) are characterized by three depressions for attachment of ligaments, one aboral and two oral. Bifacial articulations, also referred to as synarthy (Figure 1.14B), are identified by the presence of a single fossae on either side of a fulcral ridge. Variation has resulted in bifacial articulations known as cryptosynarthy, articulations exhibiting a reduction in size of the ligamentary fossae and distinctiveness of the ridge, and pseudosynarthy, articulations lacking a distinct ridge but still functioning like a synarthial articulation. The third type of movable ligamentary articulation observed is synostosis (Figure 1.14C). This is a ligamentary junction with concave faces on adjacent ossicles. This type of articulation allows for slight movement in all directions (Ubaghs, 1978a).

Five distinct types of immovable ligamentary articulations are observed in crinoids. Zygosynostosis refers to unions in which the apposed faces are nearly flat and closely fitted. A symplexy is an articulation that is crenulate, resulting in extremely limited movement. Syzygial articulations possess radiating ridges and furrows, but unlike crenularia, these are not interlocking. Instead, ridges from one articulum are in contact with ridges on the corresponding plate, with furrows opposite furrows. Two brachials united by this type of suture form a syzygial pair. The proximal ossicle is termed the hypozygal, and the distal ossicle is referred to as epizygal. In a syzygial pair, only the hypozygal ossicle has been observed to possess any specialized branching structure. It is also important to note that a syzygy, while common in the Articulata, is questionable with regards to presence in Paleozoic taxa. Symmorphial articulations are characterized by

the presence of one or two prominent ridges on one ossicle that corresponds with a socket on the opposed ossicle. Likely this type of articulation allowed for slight movement in two directions. The final type of ligamentary articulation seen is ankylosis. This is identified by an immovable union of ossicles, and commonly an observed partial or total elimination of sutures occurs (Ubaghs, 1978a).

It is generally accepted that specialized arm structures have arisen through continually modified branching of the arm rays (Figure 1.15) (Bather, 1900). These structures take the form of pinnules (Figure 1.16A), ramules (Figure 1.16B), and armlets (Figure 1.16C), and occur in a number of different taxa. The Treatise gives a short definition of pinnules, followed by numerous exceptions and modifications to allow for the variation seen in Paleozoic taxa (Ubaghs, 1978a). Pinnules, as used herein, refers to uniserial appendages projecting from each successive brachial. These appendages are roughly equal in length, and can be fixed, along with brachials, in the aboral cup. An extreme case of pinnulation is seen in some taxa later in the Paleozoic (such as the Devonian *Liparocrinus*; McIntosh, 2001). This extreme case is called hyperpinnulation, resulting in two pinnules projecting from each brachial. This pinnular state is thought to arise by single brachials carrying two pinnules, although a fusing of brachial plates during ontogeny could also be responsible for this state in some taxa. As mentioned previously, ankylosis can result in the fusion of brachials and loss of sutures.

Ramules show a less uniform pattern of arrangement, generally projecting off every second or third brachial, on alternating sides of the arm. Ramules can also vary in length over a crinoid arm. An example is seen in *Alphacrinus* (Figure 1.17), one of the earliest crinoids with disparid affinity. Ramules located proximal

to the cup extend in length to distal portion of the arm ray and are long, whereas ramules projecting from distal brachials also extend to the end of the arm ray but are short. Ramules can also be roughly equal in length, similar to pinnules. For one to distinguish between this case and pinnules, one needs to identify if the structures are originating on every brachial or if a number of brachial plates lacking this structure are present between each. Armlet spacing is similar to that seen in ramules; however, these armlets possess small appendages with further branching off individual plates.

In observing arm morphology, different clades show distinct variations that raise questions of homology and analogy. Camerate-like taxa primitively possess fixed brachials; with the entire arm ray possessing uniserial and rectangular brachials in aboral view. Through the Ordovician, these brachials become uniserial cuneate and eventually biserial. Along with becoming cuneate, pinnules begin to arise from each successive brachial, greatly increasing the filtering net cast by the arms.

Two other groups possess pinnules in the Paleozoic. Morphologically, these cladids and disparids differ greatly from the camerate clade. Initially, researchers grouped these two clades in one Linnaean sub-group: the Inadunata. It has since been proposed, and accepted, that that grouping is polyphyletic (Simms & Sevastopulo, 1993). Cladid and disparid stock differ from the camerates in reduced overall size of the calyx. A rigid tegmen, interbrachials, and fixed brachials are not present in most taxa. The brachials of these taxa begin to become cuneate, and even approach the biserial condition seen in camerates. However, they never reach the advanced state seen in many Late Ordovician camerates.

The earliest known taxa from all Paleozoic crown-clades lack pinnules. Thus, these structures cannot be interpreted as homologous. It is likely that different clades found specialized branching to be a way of increasing the area of the filter fan created by extending the arms into a current.

CT Scanning and Crinoid Arm Morphology

Computed Tomography (CT) scanning has been used for a number of years in many different fields, from medical to industrial applications. It has also found use in geology departments, in both paleontology and structural geology. The information obtained by scanning vertebrate specimens has provided not only useful information about the structure of bones still in matrix but allows researchers to create cranial endocasts and observe a slice-by-slice view of the morphology in multiple dimensions, all without destroying the specimens. However, the application of this new technology has been slow to catch on in the invertebrate community.

CT scanning works by recording different densities of the material scanned. Vertebrates possess a calcium-phosphatic based bone, with a different density compared to a siliciclastic or carbonate matrix. Unfortunately, most invertebrates possess a calcite shell or test, and they are typically found in a limestone matrix. Attempts at scanning such specimens have yielded poor results. However, one area that has shown promise for invertebrates is scanning Recent taxa and fossil taxa lacking matrix. Scanning such specimens has yielded very detailed morphology.

A fragment of a Recent crinoid arm was scanned to observe pinnule morphology. Unfortunately, little taxonomic information is known about this

specimen, nor can the arm ray, location on the arm ray, nor the collection locality, be identified. However, Sprinkle (personal communication) identified it as a reef-dwelling comatulid crinoid (Subclass Articulata) probably from the Discovery Bay area of Jamaica in the Caribbean.

Although not useful alone, this scan shows the potential for CT scanning to give us new insights about the morphology of internal structures such as the water vascular system, along with differences in stereom in individual plates. Previously, only SEM scanning allowed researchers to observe the fine stereom present in echinoderms. This scanning gave researchers a wealth of knowledge, but it was only superficial (Macurda et al. 1978). These new CT scans allow researchers to observe not only the external stereom morphology, but also the small changes that occur just below the surface. At the point of articulation the porous space becomes miminal, making identification of the fulcral ridge easy. In areas adjacent to the fulcral ridge, small pores are present, likely indicating areas of insertion for ligaments or muscles. This area of insertion does not penetrate deep into the brachial, and just behind this area the pore size present in the stereom greatly increases (Figure 1.18A). The specimen observed here possesses what appear to be oblique muscular articulations. The point of articulation between successive brachials is surprisingly minimal, with no contact between the plates both orally and aborally.

Along with providing useful information about the internal composition of crinoids, CT scanning can give new insights about external structures. The specimen observed here shows spikes present at the distal end of each pinnular plate. At the terminal pinnular, these hooks are recurved, projecting in the opposite direction of the spikes present on all other pinnulars (Figure 1.18B).

Also observed in the external view are a number of irregular plates identified as cover plates. These plates are much smaller and more irregular than those observed in Paleozoic taxa, and here are held in place by soft tissue not visible in the scan. Fine detail is also observed in the brachial-pinnule articulation point. As seen in many Paleozoic taxa, the proximal pinnulars are more robust than the distal ones, and appear to lack the spikes observed in distal pinnulars (Figure 1.18C).

As technology improves it may be possible to distinguish different compositions of calcite that would allow a more in-depth look at the construction of Paleozoic crinoids. The ability to distinguish between different types of articulations, such as muscular versus ligamentary, could provide useful data for cladistic analyses. Clearly this is one area of research that could provide many new insights about the morphology of crinoids.

CONCLUSIONS

Traditional classification of crinoids has been based on phenetics, the practice of grouping organisms with similar structures into increasingly specific groups. The classical approach is rooted in the easily defined taxa observed from the Carboniferous, but does not take into account recent discoveries from the Early Ordovician. Re-evaluation of seemingly similar structures, along with inclusion of newly discovered early Ordovician taxa, has led to new interpretations of these structures.

The column of crinoids shows, over time, a shift from somewhat unorganized pentameric construction to holomeric construction. An irregularly plated column appears to be the pleisiomorphic state in crinoids. The crinoid

calyx shows a consistent construction pattern between major clades. It is likely that an ancestral form would possess many irregular plates. Reduction and standardization of plating could eventually result in well-defined circlets with a fixed number of plates in each (usually five). This general trend can be observed by looking at some early Paleozoic taxa. Protocrinids (for example *Glenocrinus*) possess an identifiable circlet of plates at the stem-cup junction. Arm rays are present, although determination of exact location of radials is still questionable. Between these circlets, and between the inferred radials, are multiple irregular plates composing most of the calyx. Found near the same horizon, early camerate crinoids (for example *Eknomocrinus*) show a standard plating scheme for monobarthrids, though extra plates, interpreted as gap-plates, are seen in the lowest circlet. This supports a hypothesis of a reduction and standardization of circlets in the crinoid aboral cup (Guensburg and Sprinkle, 2003). Incorporation of fixed arm structures has been proposed as a specialization in crinoids, but recently described taxa possibly contradict this idea. *Alphacrinus*, the earliest disparid yet known, has a few fixed brachials incorporated into the top of the cup (Guensburg, 2010). A similar condition is seen in early camerates and the protocrinids.

Anal structures in crinoids differ between various clades. Most workers accept that the camerate anal series is not homologous to that seen in the disparids and cladids. The latter two clades vary in anal structure, but based on morphological analysis, are thought to be homologous. Undoubtedly the question of homology and homoplasy is crucial to a better understanding of the relationship between the different clades, and the origins of crinoids as a whole.

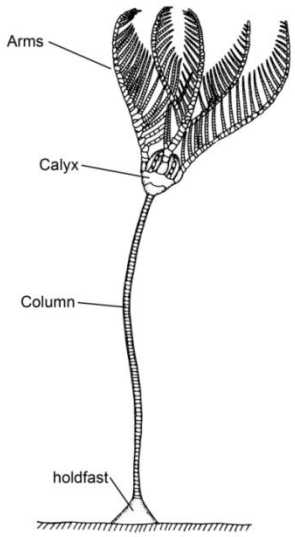

Figure 1.1: Basic morphology of a stalked crinoid (modified from Barnes (ed.) 2001)

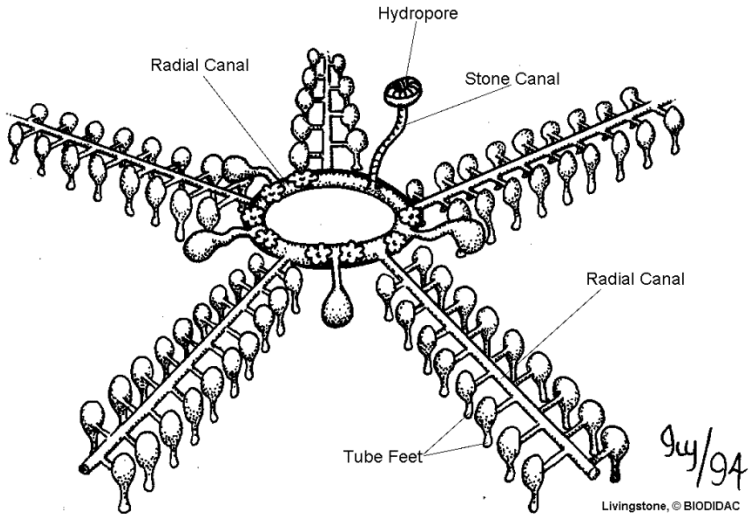

Figure 1.2: Morphology of the water vascular system in echinoderms as exhibited by a sea star (modified from BIODAC, original sketch by Ivy Livingstone, 1994).

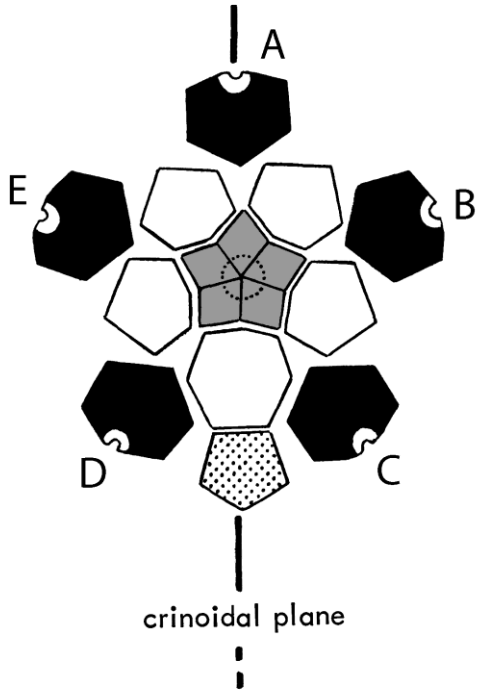

Figure 1.3: Orientation of bilateral symmetry and ray pattern in crinoids. Radial plates black, basal plates white, infrabasals grey, anal plate stippled (modified from Ubaghs, 1978a).

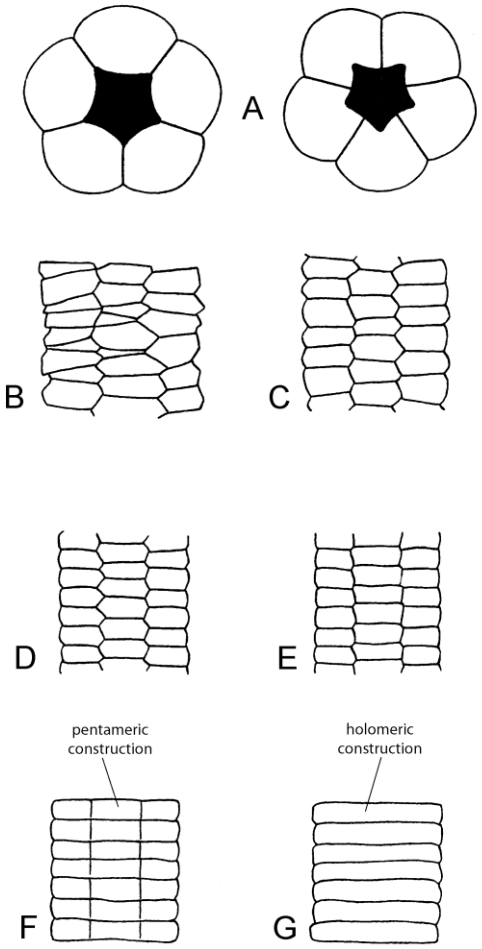

Figure 1.4: Column construction in Paleozoic crinoids (modified from Ubaghs, 1978a). (A) Pentameric column in transverse sections showing different orientations of axial canal angles, (B-G) diagrammatic morphologic series showing hypothesized evolution of column from irregular plates (B) to irregular and alternating (C, D) to regular and oriented in horizontal rows and (G) finally holomeric construction.

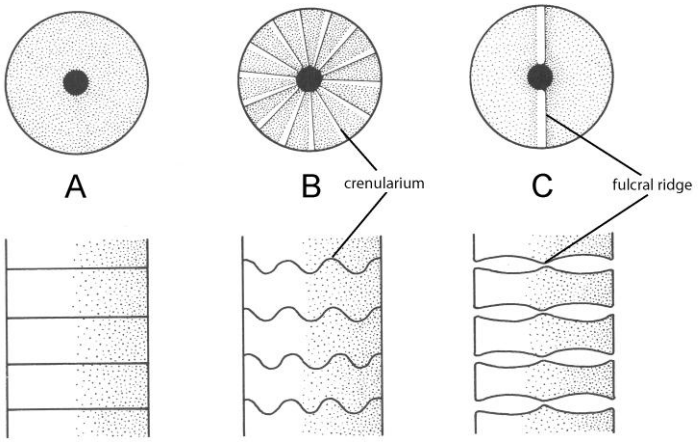

Figure 1.5: Types of articulation facets observed in crinoid columns, top row depicts columnal surface in transverse view, bottom row shows lateral view of columnals composed in a short segment of column. (A) Synostosis, (B) symplexy exhibiting crenularia, (C) synarthy exhibiting a fulcral ridge (modified from Ausich et al., 1999).

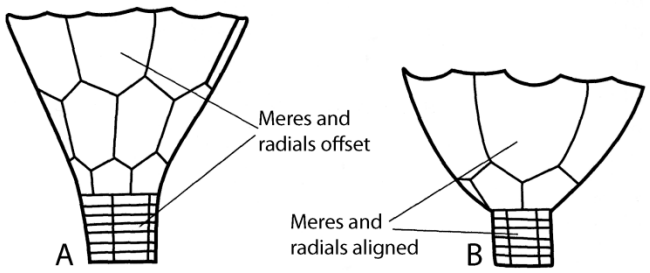

Figure 1.6: Depiction of the "Law of Wachsmuth and Springer" with cup in lateral view (modified from Guensburg and Sprinkle, 2003). (A) Three circlet cup with stem meres aligned and radials offset, (B) Two circlet cup with stem meres and radials aligned.

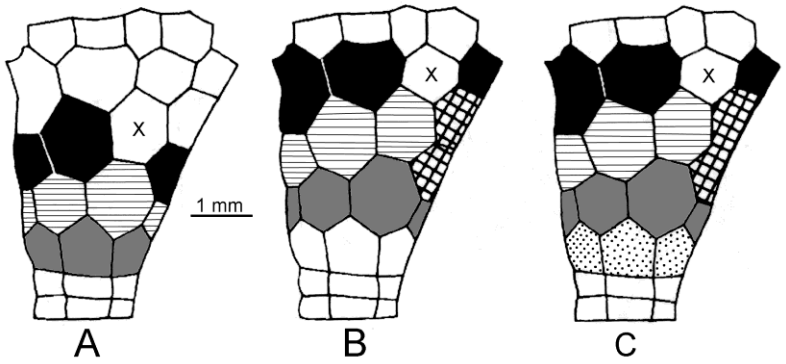

Figure 1.7: Three interpretations of plate homologies in *Aethocrinus moorei*, illustrated in D-ray view (modified from Ausich, 1996). Radial plates black, basal plates horizontally striped, infrabasals grey, lintels stippled, cross-ruled pattern indicates infer- and superradials, X is anal X. (A) Ubaghs 1968, dicyclic cup with lowest circle infrabasals, (B) Philip and Strimple 1971, dicyclic cup with lowest circlet stem meres (C) Ausich 1996, Tricyclic cup with lowest circlet lintels.

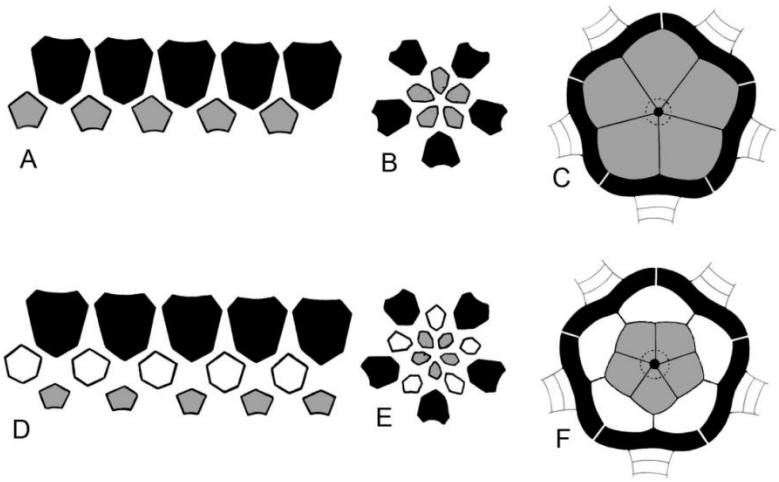

Figure 1.8: Three differing ways of representing basic calyx structures in crinoids with monocyclic (A-C) and dicyclic (D-F) bases (diagram style modified from Ubaghs, 1978a). Radial plates black, basal plates white, infrabasal plates grey (based on homology scheme proposed by Guensburg and Sprinkle, 2003).

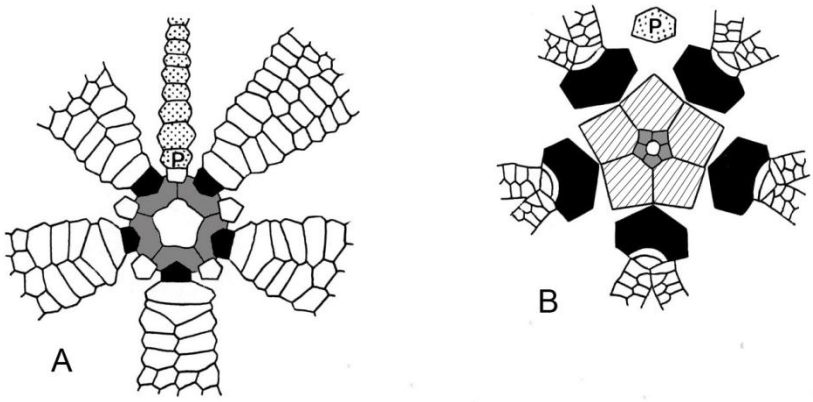

Figure 1.9: Orientation of anal structure in camerate crinoids (modified from Ubaghs, 1978a). Radial black, anal plates stippled, P is primanal. (A) *Cleiocrinus* (Billings), Late Ordovician, N. America, (B) *Nyctocrinus* (Springer), Middle Silurian, N. America.

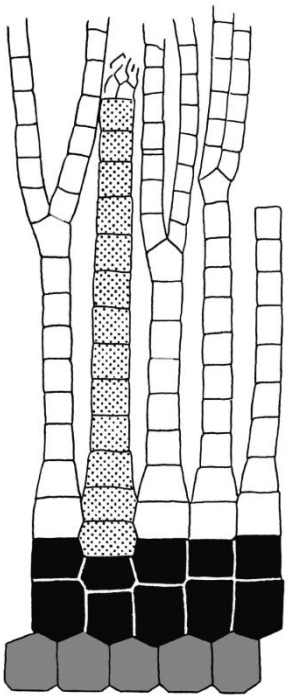

Figure 1.10: Orientation of anal structure in the disparid crinoid *Eustenocrinus springeri* (Ulrich), Late Ordovician, Canada. (Modified from Ubaghs, 1978a) Brachial plates black, anal plates stippled.

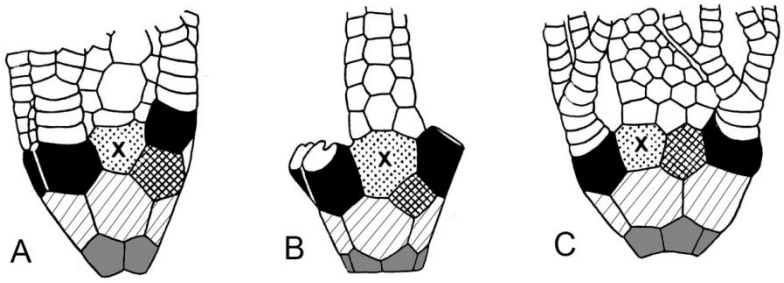

Figure 1.11: Orientation of anal structure in cladid crinoids. (Modified from Ubaghs, 1978a) Radial plates black, radianal cross ruled, anals stippled, X is anal X. (A) *Cupulocrinus humilis* (Billings), Upper Ordovician, N. America, posterior view, (B) *Thenarocrinus gracilis* (Bather), Middle-Upper Ordovician, Canada, USA, Estonia, posterior view, (C) *Botryocrinus cucurbitaceus* (Angelin), Middle Silurian, Sweden, posterior view.

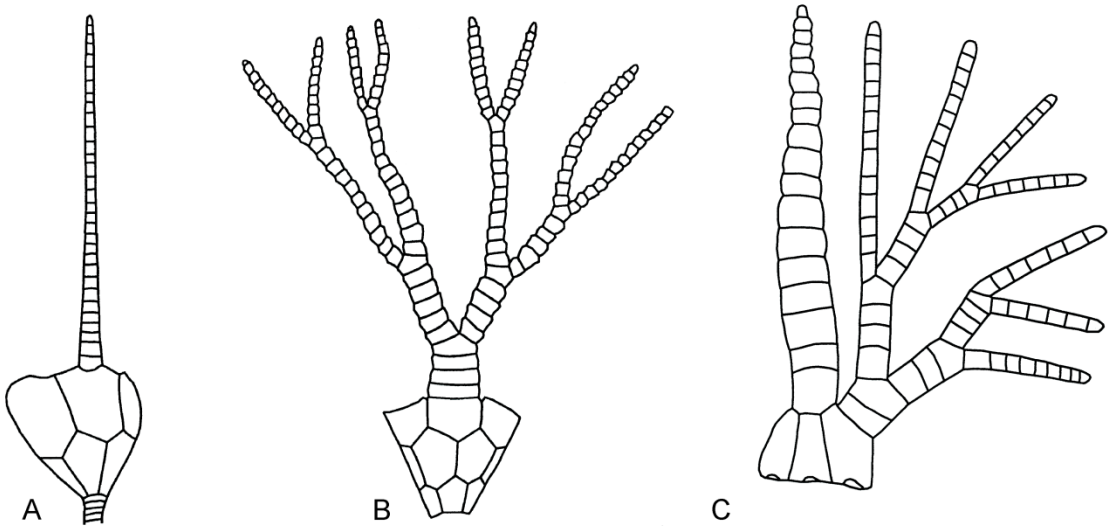

Figure 1.12: Types of arm branching observed in crinoids (modified from Brower, 2006). All figures shown in aboral view with a single ray in food gathering position. (A) Atomous branching (*Hybocrinus conicus* Billings), (B) isotomous branching (*Cupulocrinus crossmani* Brower), and (C) heterotomous branching (*Cremacrinus ramifer* Brower).

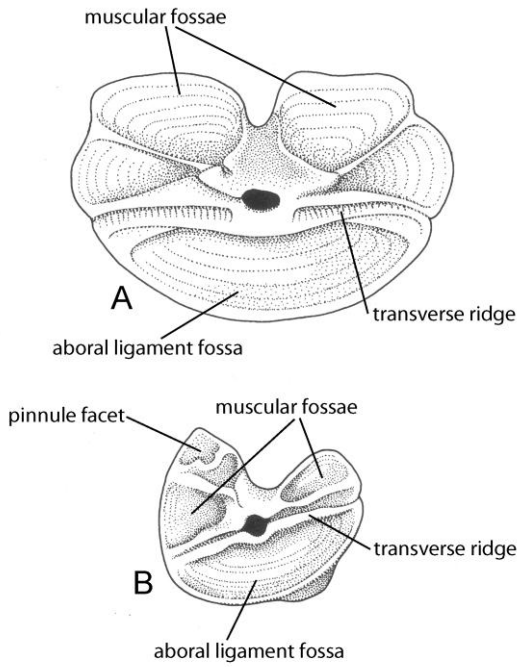

Figure 1.13: Muscular articulations of *Marsupites testudinarius*, Upper Cretaceous, Europe. (Modified from Ausich et al., 1999). (A) Straight muscular articulation, (B) oblique muscular articulation.

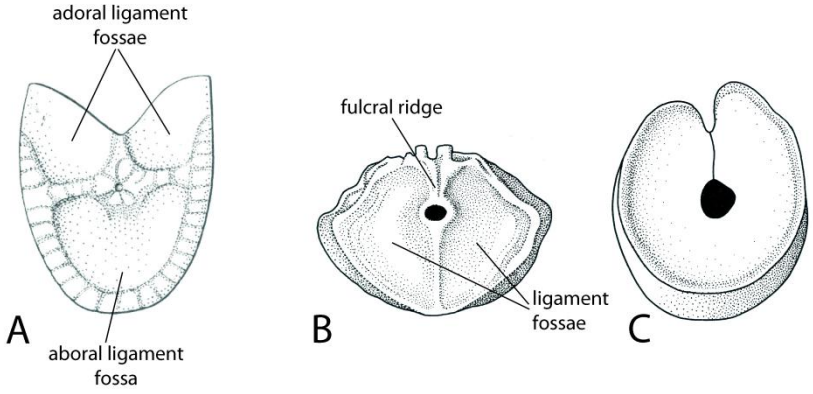

Figure 1.14: Major types of movable ligamentary articulations observed in the crinoid arm (modified from Ubaghs, 1978a). (A) Trifacial articulation (B) Synarthy (bifacial articulation (C) Synostosis.

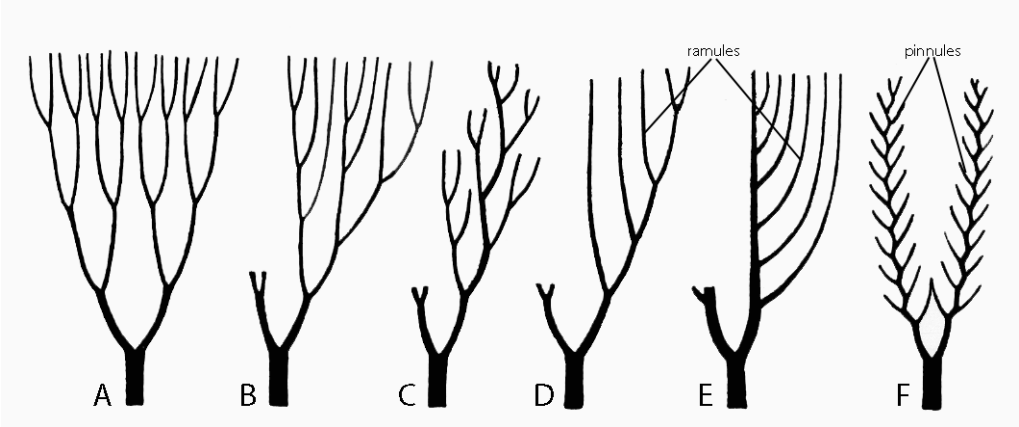

Figure 1.15: Proposed evolution of specialized arm structures through continual modification of branching (modified from Bather, 1900). Branching pattern terminology: (A) isotomy, (B) heterotomy, (C) bilateral heteromy (D) endotomy, (E) ectotomy, (F) holotomy (terminology from Fearnhead, 2008).

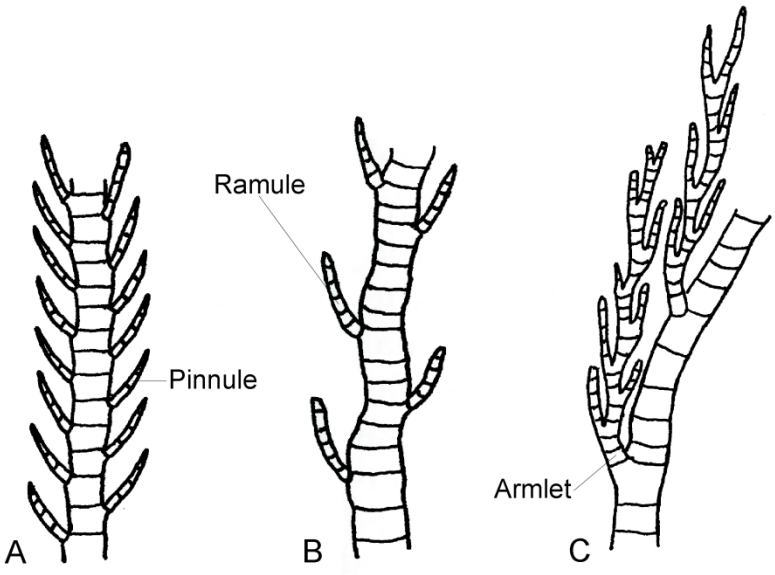

Figure 1.16: Types of specialized arm structures observed in Paleozoic crinoids (modified from Webster and Maples, 2008). (A) Uniserial arm bearing pinnules, (B) uniserial arm bearing ramules, (C) uniserial arm bearing armlets.

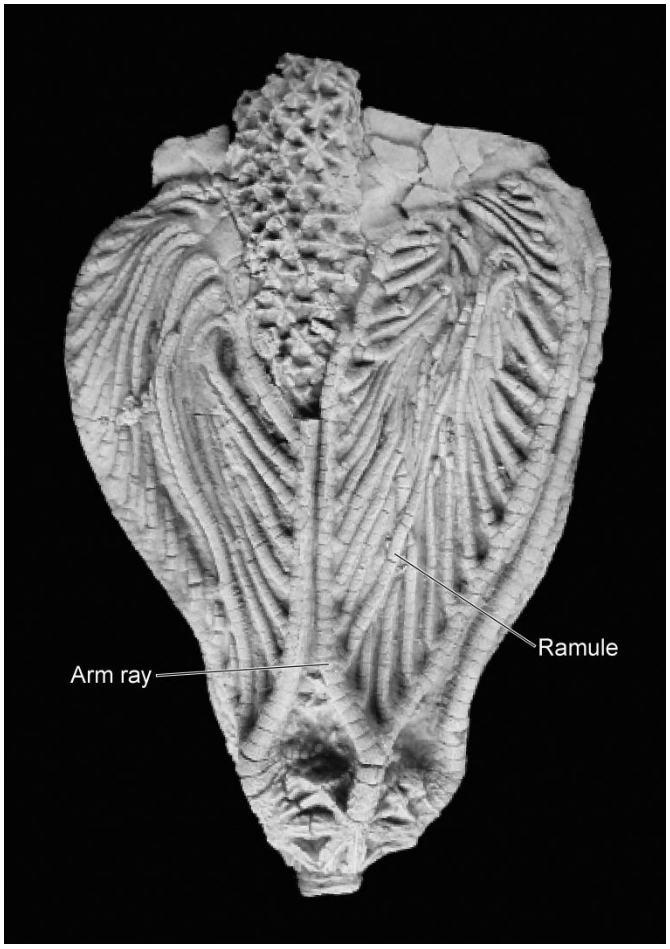

Figure 1.17: *Alphacrinus mansfieldi*, showing elongated ramules extending to the distal tips of arm rays (from Guensburg, 2010).

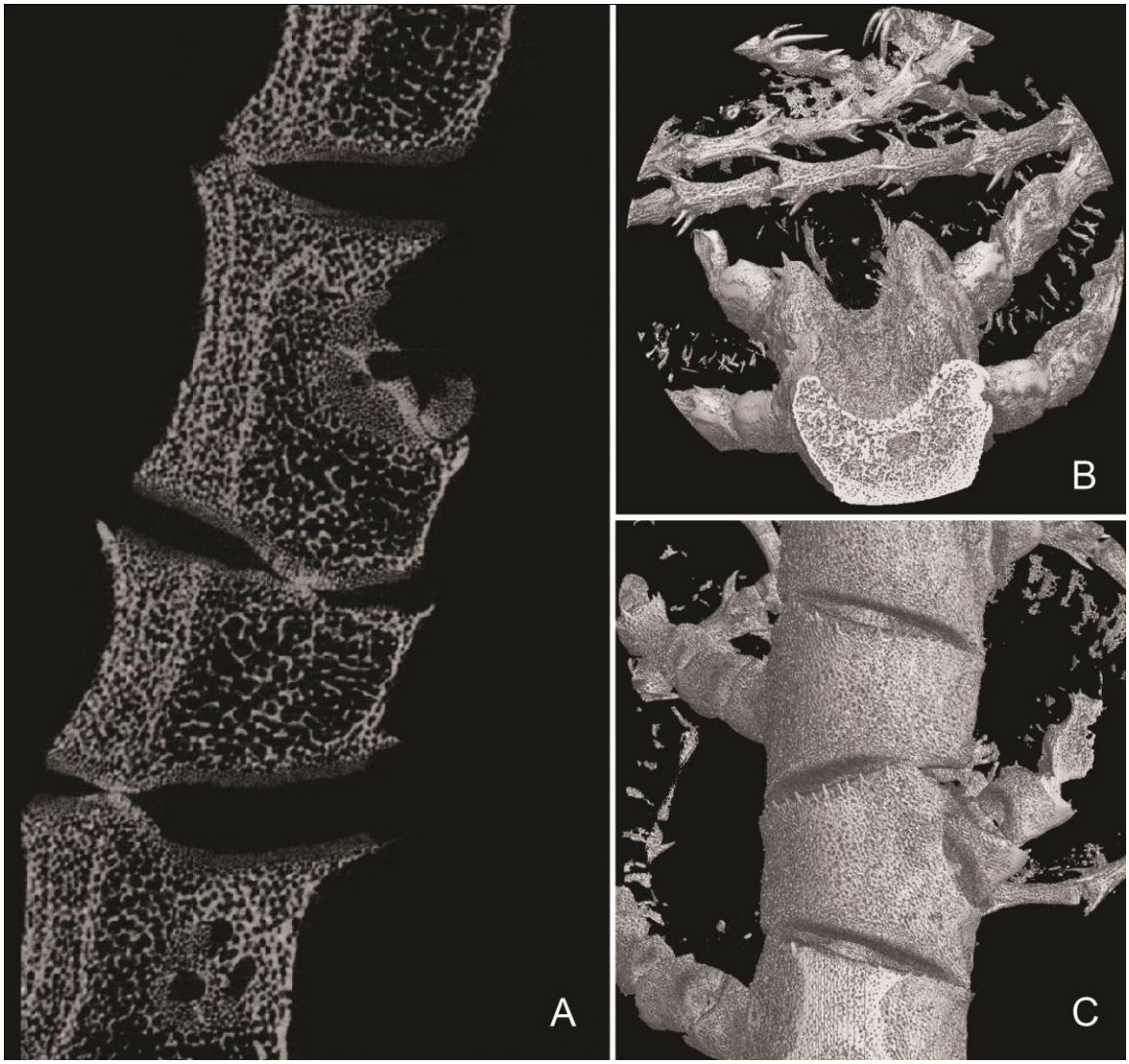

Figure 1.18: Images of a Recent crinoid arm obtained through Computed Tomography scanning (much enlarged). (A) Slice of arm showing varied density of stereom in brachials, (B) external view of arm in cross section showing pinnules with spikes on distal edges and cover plates, and (C) external view of arm and pinnule attachments in aboral view.

Chapter 2: *Cladistic analysis of crown group crinoids*

HISTORY OF CLASSIFICATION

Work concerning fossil crinoids dates back to the middle of the 16th century, well before the development of a nomenclature system and even before the recognition of crinoids as distinct group of animals (Ausich & Lane, 2006). Despite the lack of conserved terminology, observations made in this time are still useful in the identification of certain types of distinctive columnals. Names such as *Pentacrinites* were coined in the 16th century and are still used today. However, much of what we now take for granted in the biological sciences, ideas such as evolution, extinction, functional morphology, cladistics, and plate tectonics, have allowed for more rigorous analysis of relationships among organisms.

It was in 1821 that the term Crinoidea was first applied to a group of organisms. Members of this group were defined as “Animals with a round, oval, or angular column, composed of numerous articulating joints, supporting at its summit a series of plates or joints forming articulated arms, dividing into tentaculated fingers, more or less numerous, surrounding the aperture of the mouth, situated in the center of a plated integument, which extends over the abdominal cavity, and is capable of being contracted into a conic or proboscal shape” (Miller, 1821). Though the group name carried no Linnaean rank, the Crinoidea was split into four divisions based on suture structure within the calyx. Unfortunately, this terminology was slow to be accepted in the scientific community. The slow speed at which information travelled did not help. Competing scientists were also more likely to use terminology from their native country rather than adopt another’s.

During the early days of crinoid paleontology, there were two schools of study. One of these groups was composed of the English scholars. These researchers came to paleontology from the field of biology. Having a traditional background in biology, these scientists had studied modern crinoids and were able to apply this knowledge to the fossil taxa. The second school of study was composed of amateur paleontologists in the United States. These researchers worked in their free time to study and describe fossil crinoids. These two schools came to different conclusions about what structures are important and useful in classifying specimens. Though not as well versed in the scientific method as their English counterparts, the American workers of this time did have an advantage in the abundance of well-preserved crinoids from the American mid-west. Two American workers who had a great impact on the study of crinoids were Charles Wachsmuth and Frank Springer.

In the 1880's Wachsmuth began working with Springer on crinoids, specifically on Paleozoic groups. Grouping all Paleozoic crinoids within the order Paleocrinoidea, these workers formally recognized three families within the order. These families were the Icthyocrinidae, Cyathocrinidae, and Sphaeroidocrinidae (Wachsmuth and Springer, 1878, 1881). These groupings were based on construction of the oral surface, calyx plating (specifically anal structures), and the construction of arm rays and the stem. Wachsmuth and Springer eventually revised these names to form the orders Inadunata, Camerata, and Articulata.

Around this time, new workers in Europe began proposing their own ideas about crinoid relations. Francis Bather, an English scientist, argued that previous schemes created a diphyletic grouping of crinoids. His main focus was the aboral cup plating pattern, and he proposed the new subclasses Monocyclica

and Dicyclica (Bather, 1899). This division was similar to the orders proposed by Wachsmuth and Springer, though the terminology required for describing specimens became increasingly complicated, requiring two to three terms together to correctly identify specimens.

Congruent to this work Otto Jaekel, a German paleontologist, divided the Crinoidea into three subclasses. These he termed Eocrinoidea, Cladocrinoidea, and Pentacrinoidea. Divisions here are based on the assumption that arm structures in the different crinoids are not homologous. The Cladocrinoidea, in Jaekel's classification, was analogous to Wachsmuth and Springer's Camerata, and Pentacrinoidea to Inadunata. Subclass Eocrinoidea refers to post-Paleozoic taxa (Jaekel, 1918).

These workers laid the foundation for what we know today, but it took researchers until the 1940's to take the accumulated knowledge from different workers in different countries and create a singular idea of crinoid relationships. This task was taken up by Raymond Moore and Lowell Laudon, publishing *Evolution and Classification of Paleozoic Crinoids* in 1943.

Fundamental to classifying Paleozoic crinoids was the identification of criteria useful in evaluation. Understandably, different structures have differing levels of importance in showing progressive evolutionary modification and in giving reliable indication of relationships (Moore and Laudon, 1943). Declining to support Bather's proposed importance on the number of circlets in the aboral cup over other structures, Moore and Laudon proposed that the extent to which lower ray plates are incorporated in the calyx is significant in classification, but plates of corresponding position in the rays are homologous in all types of crinoids. Variation in the structure of an anal series between camerates and 'inadunates'

helped to support the division of these two groups, and again refuted Bather's ideas about division in the Crinoidea.

With the publication of the *Treatise on Invertebrate Paleontology* (Moore & Teichert, 1978) future students of crinoid paleontology finally had a "holy grail" containing all the information about crinoids known up to the early 70's. Unfortunately for researchers in the 21st century, ideas have changed and the *Treatise* has not yet caught up. Major changes include the dissolution of Inadunata and elevation of Cladida and Disparida to the same level as the Camerata (Simms and Sevastopulvo, 1993).

THREE NEW INTERPRETATIONS OF CALYX PLATE HOMOLOGIES

One area that has received increased attention from researchers deals with homology schemes between the different groups. The basis for recent studies of crinoid relationships has revolved around differences in thecal plating homology. The aim of evaluating such structures is to understand the relation of crown groups to one another. The first competing scheme of plate homology to differ from that used by researchers for almost 100 years was first proposed in the early 1990's (Simms, 1994). Rather than focusing on the attachment of arms to the calyx, it proposed that the attachment of stem to cup was of key importance (Simms, 1994). The basis for this new interpretation was found in the 'Law of Wachsmuth and Springer', which states that in tricyclic cups radials and stem meres are offset, whereas when a cup shows a two-circlet organization, the radials and meres align. A constant orientation of stem symmetry to the lower circlet plates is observed in the great majority of two- and three-circlet taxa. Further, it is proposed that the difference in orientation of arms relative to the

stem was caused by the presence or absence of the uppermost circlet. Therefore, this scheme differs from that in the *Treatise* by the presence or absence of radial plates rather than the presence or absence of infrabasal plates (Figure 2.1).

Another homology scheme was proposed in the late 1990's (Ausich, 1996). This new proposal was supported by the following assumptions: (1) the ancestral crinoid had a calyx composed of four primary circlets, (2) any circlet of plates can be lost, (3) initial suturing of plates determines orientation (before suturing, plates adjust to 36 degree alternating positions, whereas after suturing plates remain in relative positions), and (4) the only important symmetry relationship between the column and calyx is the relationship between the lumen angles and the lowest circlet in the aboral cup (Ausich, 1996). These assumptions were combined with a new description of the troublesome taxon *Aethocrinus moorei* (Ubaghs, 1969). *A. moorei* is reinterpreted as a four-circlet crinoid; with a circlet of plates below the infrabasals termed the lintel plates. The lintel plates of *A. moorei* are aligned with the stem meres, leading previous researchers to identify them as such (Philip and Strimple, 1971). The argument for the use of the term lintels is based on the orientation of the column lumen with respect to the lowest circlet, rather than the rotation of 36 degrees between the top-most mere and the lowest circlet. The presence of this characteristic allowed the removal this taxon from the cladid-stock and the creation of a new sub-class, the Aethocrinida (Ausich, 1998). The formation of this new grouping is supported by new interpretations of other four circlet crinoids, *Perittocrinus* and *Tetracionocrinus* (Ausich, 1996).

Based on a four circlet ancestor, disparids are proposed to be lacking a basal circlet. Radial facets, in this system, appear on whatever radially oriented plate was present when the arms began to differentiate (Ausich, 1996). Therefore, disparids with “compound radials” in the traditional system have arms originating on radial plates. Those lacking compound radials have the arms originating on the infrabasal plates. This system retains the disparids as a single clade (Ausich, 1998). If this interpretation is not correct, some members of the disparid stock retain plates homologous to basals and radials of other crinoids, forcing the division of this clade into two. Also, a previous interpretation (Simms, 1994) about proximal-most posterior (anal) plates applies to the disparids. Terminology for all groups except for the disparids remains identical to that of the traditional scheme (Figure 2.2).

A third homology scheme was recently proposed, this scheme being based on a dual reference system (Guensburg and Sprinkle, 2003). This approach conserves two important junctures in the functional morphology of crinoids, the stem-cup junction and arm-cup junction. It is the basal plates that are present or absent in the calyx. Therefore all stalked crinoids should possess a stem attaching to infrabasal pates, and arms originating on radials, with basals present or absent (in three-circlet and two-circlet forms, respectively) (Figure 2.3). The hybocrinids possess unique cup morphology in this system. It is proposed that the original cup-base is secondarily lost or a stem mere is added to the base, resulting in a “pseudomonocyclic” cup (Warn, 1975; Guensburg & Sprinkle, 2003). I am in agreement with those authors with regards to the lintel plates. The term lintels should be retained but used only in cases where stem meres have been incorporated into the cup.

HISTORY OF CRINOID CLADISTIC ANALYSES

A cladistic analysis is a particular method of hypothesizing relationships among organisms based on the idea that members of a group share a common evolutionary ancestor. It differs from phenetic classification because of this evolutionary aspect. The key to producing a successful cladistics analysis is discerning between homologous and analogous characters. It is important to understand the three types of characters used in cladistic studies. Plesiomorphic characters are those present in ancestral taxa. Synapomorphic characters are newly derived characters that are shared by two or more taxa. Autapomorphic characters are unique characters observed only in a single taxon. Plesiomorphic characters are important for defining an outgroup and rooting the tree. Synapomorphic and autapomorphic characters give the tree its topology, or branching pattern.

Cladistic analysis was quick to be adopted in the paleontological study of vertebrates, plants, and even insects. Its application to other groups of invertebrate organisms, specifically those lacking useful molecular information, has been slow and often unreliable when applied. In attempting to elucidate the relationship between the major crinoid groups different authors have applied different assumptions, varied outgroup selection, and included or excluded various taxa. Three cladistic studies, published over the past 20 years, are analyzed below. At the core of each of these studies is a proposed new plate homology scheme for the aboral cup (discussed above).

In the past decade workers investigating some of the oldest Ordovician rocks have discovered a number of crinoids with affinities to one crown group or another, while at the same time possessing a number of plesiomorphic

structures. The difficulty of placing these within the accepted groupings has lead researchers to propose yet more sub-classes, such as the Aethocrinids and Protocrinids (Ausich, 1998; Guensburg & Sprinkle, 2003, respectively). These discoveries, along with the previously discussed homology issues, have led to confusion about early relations of these groups.

Three cladistic analyses have attempted to resolve relationships between different crown groups of crinoids (Simms, 1993; Ausich, 1998; Guensburg & Sprinkle, 2003). Each analysis has resulted in a different topology. There are three main reasons these cladograms differ; each study implemented a new plating homology scheme, outgroup selection has varied, and characters used in analyses differed.

The first study conducted (Simms, 1993) selected *A. moorei* as the outgroup, based on the presence of a circlet of plates below the infrabasals. The tree produced in this study is referred to in the literature as a cladogram (Figure 2.4), although no information is presented with regards to analysis parameters. Also, a data matrix with character states it not given in the literature. The terminal taxa of this study are represented by: genus, family, class, and subclass levels of the Linnaean hierarchy. Nine terminal taxa are presented, with a total of fifteen characters.

The topology of the tree obtained in this study recovered two monophyletic clades. Cladid-like taxa branch off first and create a single clade. The camerates are paraphyletic in this study, giving rise to the monophyletic disparids. These clades are proposed to be originating from a primitive *Aethocrinus*-like taxon. This interpretation removes *A. moorei* from the cladids and makes use of it as the outgroup. The cladid clade is suggested to be derived

by the loss of the lowest circlet of plates. The camerate-disparid clade arose from the cladid clade through the loss of the radianal plate from the theca. Camerates further evolved a unique collection of characters, whereas the disparids are proposed to have experienced a paedomorphic decrease in thecal complexity (Simms, 1993).

The second study of interest (Ausich, 1998) selected *Caryocystites,* a rhombiferan cystoid, as the outgroup based on the presence of a four circlet theca. This is not meant to be a direct ancestor to crinoids (as it appears later in the geologic record than many taxa analyzed), but rather a hypothetical representative of the ancestral stock. Analyses were carried out using PAUP*, with all characters unordered and equally weighted. All searches were run with ten random-addition-sequence replicates. Trees were constructed using a 50% majority rule when more than a single tree was obtained (Ausich, 1998). Taxa represented in this study are identified to the species level. 32 taxa were selected, and 25 characters coded.

The tree obtained (Figure 2.5) indicates the Aethocrinid stock represents the most basal construction for crinoids, in agreement with observations made by Simms. However, this is the only similarity in topology for both trees. This study suggests camerates and cladids form two monophyletic clades and are sister taxa. This grouping is supported by both groups losing the lowest circlet of plates, the lintels (based on Ausich's homology system). The camerate/cladid clade is the sister group to the disparids. Disparids are thought to have undergone a reduction in the calyx as well, though here they are characterized by the loss of the basal circlet, primitively retaining radials, basals, and lintels. The "superradial/inferradial" condition is interpreted as a loss of the basal circlet

and consequent juxtaposition of two radial oriented circlets, the radials and infrabasals. Taxa lacking this “biradial” condition are thought to have lost the radial circlet, with arm facets now appearing on the infrabasal circlet (Ausich, 1998).

This analysis argues that *A. moorei* represents the ancestral condition of crinoids. It makes no use of some of the oldest known crinoid specimens. These are Early Tremadocian in age and show a somewhat standard, yet pleisiomorphic plating scheme. It is likely that the Aethocrinidae do not represent an ancestral condition, but are rather an evolutionary offshoot of a more standard stock that was present a slightly later time.

The third analysis was able to make use of some of these newly discovered taxa, and employs the protocrinids as an outgroup (Guensburg and Sprinkle, 2003). This taxon shows many characteristics considered to be pleisiomorphic for crinoids; a pentameric stem, an irregular mulit-plated dorsal cup, fixed brachials and interbrachials, and uniserial, nonpinnulate, isotomous arms. The result of this cladistics analysis is yet another interpretation of crown group relations (Figure 2.6). Based on this, camerates are the first group to branch off. Camerates are characterized in this study by extensive interbrachial plating and anal plating confined to the CD interray (Guensburg & Sprinkle, 2003). The canerate grouping is paraphyletic in this analysis. Both disparids and cladids produce monophyletic clades, and both are present higher in the tree based on their reduced cup plating.

In the three studies reviewed above, each results in a different relationship between the crown groups. The first places the cladids as the basal-most member, with the camerates and disparids represented as more derived sister

taxa. The second suggests the disparids branch away first, represented as a single monophyletic clade. Cladids and camerates are also monophyletic in this study, and they are represented as sister clades. The third makes use of newly described protocrinids as the outgroup. Here the camerates branch off first and are paraphyletic. The cladids and disparids are sister taxa and are retained in two monophyletic clades. These two clades are distinguished by a reduction in thecal plating.

Three differing homology schemes, three different outgroup selections, and three different topologies are laid out in these studies. This presents a problem for those interested in studying the origin and diversification of crinoids. The application of respective homology schemes has continued by different researchers. With the conservation of terminology, readers must understand all schemes and how to reinterpret descriptions based on their own understanding of homology.

NEW ANALYSIS

For this analysis taxa from only the Early Ordovician were selected. Taxa had to score for over 75% of data to be included in the analysis. This means taxa lacking arms, stem, or poorly preserved to the point where identification of structures was unidentifiable were omitted. Taxa omission is justified because the presence of numerous, ambiguous taxa result in largely unresolved trees that give little insight toward crinoid relationships.

The analysis was carried out using 11 taxa. 16 characters were coded (character and state definitions in Appendix A) (data matrix presented in Appendix B), each character is unordered and equally weighted. A heuristic

search was conducted using PAUP version 4.0b10. A heuristic search was carried out using simple addition sequence. Four most parsimonious trees were obtained, each with a tree length of 36. A strict consensus tree was produced (Figure 2.7). Values obtained indicate a Consistency Index (CI) of 0.765 when uninformative characters are removed. The retention index (RI) value is 0.784, and the rescaled consistency (RC) index value is 0.599. These values support the topology obtained from this study.

Outgroup selection, as observed in previous analyses, can have a major effect on tree topology. In determining an outgroup, one needs to think about what could likely be ancestral to crinoids. For this analysis, the protocrinids are placed as the outgroup. This group is selected based on the presence of many plesiomorphic structures and an early occurrence. Though defined circlets are present at the stem-cup junction and arm rays extend down to (inferred) radials, the plates between are small and irregular in orientation. Also present are fixed brachials, interbrachials, a pentameric column, and uniserial isotomous arms lacking pinnules.

The issue of plate homology schemes was avoided in the study by only identifying the number of circlets present, rather than defining the presence or absence of circlets as individual characters. It is important to note that based on a review of the morphology of crinoids, this author accepts that the dual reference system for crinoid plate homology (Guensburg & Sprinkle, 2003) as the most logical system proposed. This is accepted based on the idea that functionally important sites, where the column and cup come into contact or where the arms extend away from the calyx, are conserved. Based on the notion that a single ancestor gave rise to all crinoids, these sorts of functional sites

should be homologous among crinoids. Further evidence to support this homology scheme is observable in the pleisiomorphic protocrinids. Only two well defined circlets are present in this group, the infrabasals at the stem-cup junction and the radials that give rise to the arms.

The results of this analysis keep crown groupings intact, and produce monophyletic clades for all crown groups. A single taxon appears problematic, *Alphacrinus mansfieldi*, Guensburg, 2010, is placed as the sister group to the large clade containing the disparids, cladids, and hybocrinids. The location of this taxon is based on the presence of plesiomorphic structures; including interbrachial plates, and arm branching occurring before the arms become free. This specimen has been described as an early disparid. This analysis indicates, if correct, that this taxon represents a primitive condition for disparids, and further supports a hypothesis of reduction in plating as a general trend in crinoid evolution.

The placement of a highly reduced group, the hybocrinids, further supports the hypothesis of reduction as a trend in crinoids. Different authors have proposed this group arose from disparid stock (Ausich, 1998), whereas others have supported the hypothesis that hybocrinids arose from cladid stock (Sprinkle, 1982; Guensburg & Sprinkle, 2003). The results of this current analysis support the latter interpretation. However, the hybocrinids here are not considered a monophyletic grouping at the level of the camerates, cladids, and disparids. This is due to the presence of a single hybocrinid taxon in the analysis.

DISCUSSION

Although the topology of the tree obtained using protocrinds as the outgroup does retain crown groups, the author feels there is still a question about crinoid origins. New higher echinoderm taxa always appear suddenly, possessing well-formed bauplans, with no intermediate forms (Rozhnov, 2007). It has been proposed by some that these observations are due to rapid morphological change over small geologic intervals. This has resulted in some researchers suggesting that the crinoid bauplan originated very early in the Ordovician. Paleobiogeographic studies (see following chapter) suggest it is unlikely that the crinoid bauplan originated in the Early Ordovician, based on dispersal of taxa in the Tremadocian.

Forcing the outgroup to be a rhombiferan cystoid (see Ausich, 1998) results in the retention again of crown groups**,** although the topology is completely inverted with respect to the initial tree obtained. Rather than a trend of reducing and standardizing plate over time, this cladogram showing different trends of increasing and decreasing complexity in different clades.

A major force orienting the topology of both trees then becomes definition of outgroup. Protocrinids have many affinities that place them near and likely basal to camerates. Through a reduction of plates and simplification of calyx plating one could derive the camerates. Further reduction results in the cladids and disparids. Rhombiferan cystoids show a reduced plating of the theca when compared to camerates. The result of applying a rhombiferan cystoid as the outgroup taxon is that cladids branch off first and form a paraphyletic clade. Disparids and camerates are sister taxa, and the protocrinids appear at the top of

the tree, indicating the presence of an irregular, multi-plated calyx as derived rather than ancestral.

For this study, only a handful of the taxa of interest were available for direct study. Character states for the remaining taxa were obtained from primary literature. A comprehensive re-evaluation of taxa based on first-hand observations would help an analysis of this nature. Attention should be given to understanding suture structures in all plates. Small, and often difficult to observe, structures such as cover plates and food groove characteristics are too often omitted from formal descriptions. Also, a study of the types of articulations present in different taxa has the potential to yield a number of informative characters. A systematic approach to describing crinoids has recently been proposed (see Fearnhead, 2007), but it has not come into wide use as of yet.

CONCLUSIONS

The analysis herein presents the first step toward creating a comprehensive phylogeny for Paleozoic crinoids. The next step in this line of research is to reduce the amount of confusion currently present with the terminology observed in different crown groups of crinoids. At the present time, morphological features are described for crinoids as a whole. This creates a problem as to what structures are homologous versus analogous. For example, if pinnules are not present in any of the earliest representatives of all crown groups, how can the same structure appear in different clades later in time? Furthermore, if pinnules are the final product of arm branching, should they not be referred to with respect to arm branching, rather than as a unique structure on the arms? Genetic and functional constraints have likely limited the types of

structures that could have formed in crinoids, but a clear divergence of crown groups in the Early Ordovician suggests structures observed are in fact analogous.

The cladistics analysis retains three crown groups, the Camerate, Cladid, and Disparid clades. These groupings have historically been based on the plate homologies observed in the aboral cup. Hybocrinids are located within the Cladid clade. The results of this cladistic analysis are congruent with historical groupings, even with the omission of plating homologies. Aboral circlet terminology was purposely omitted to remove any sort of bias that would be presented by an incorrect interpretation.

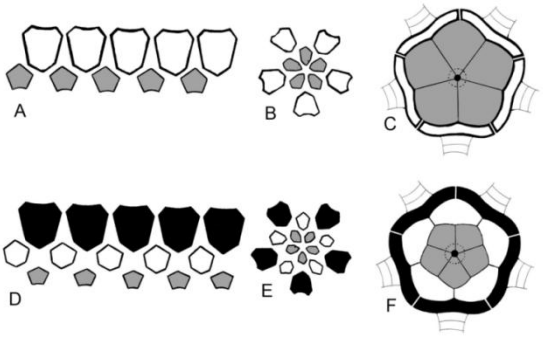

Figure 2.1: Plate homology scheme as proposed by Simms, 1994. A, B, C, represent aboral cup with two circlets present, D, E, F, represent aboral cup with three circlets present (based on diagram modified from Ubaghs, 1978). Black plates indicate radials, white plates indicate basals, grey plates indicate infrabasals.

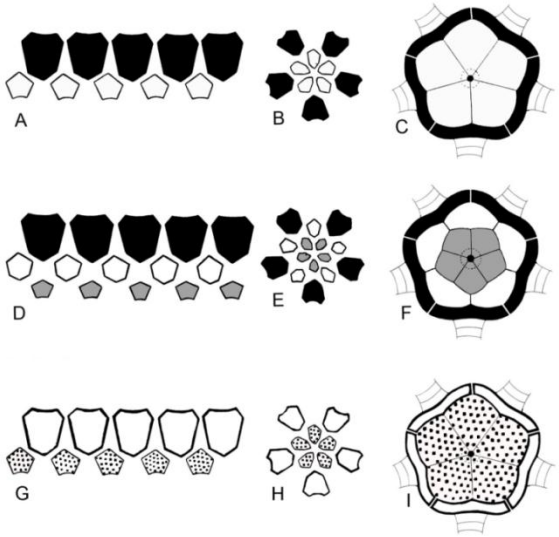

Figure 2.2: Plate homology scheme as proposed by Ausich, 1996. A, B, C, represent aboral cup with two circlets present, D, E, F, represent aboral cup with three circlets present. G, H, I represent aboral cup of disparid with simple radials (based on diagram modified from Ubaghs, 1978a). Black plates indicate radials, white plates indicate basals, grey plates indicate infrabasals, stippled plates indicate lintels.

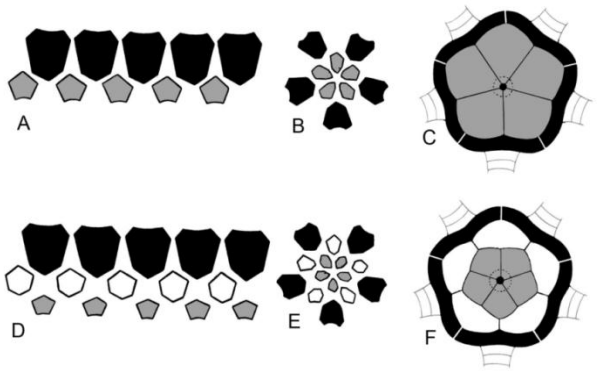

Figure 2.3: Plate homology scheme as proposed by Guensburg & Sprinkle, 2003. A, B, C, represent aboral cup with two circlets present, D, E, F, represent aboral cup with three circlets present (based on diagram modified from Ubaghs, 1978a). Black plates indicate radials, white plates indicate basals, grey plates indicate infrabasals.

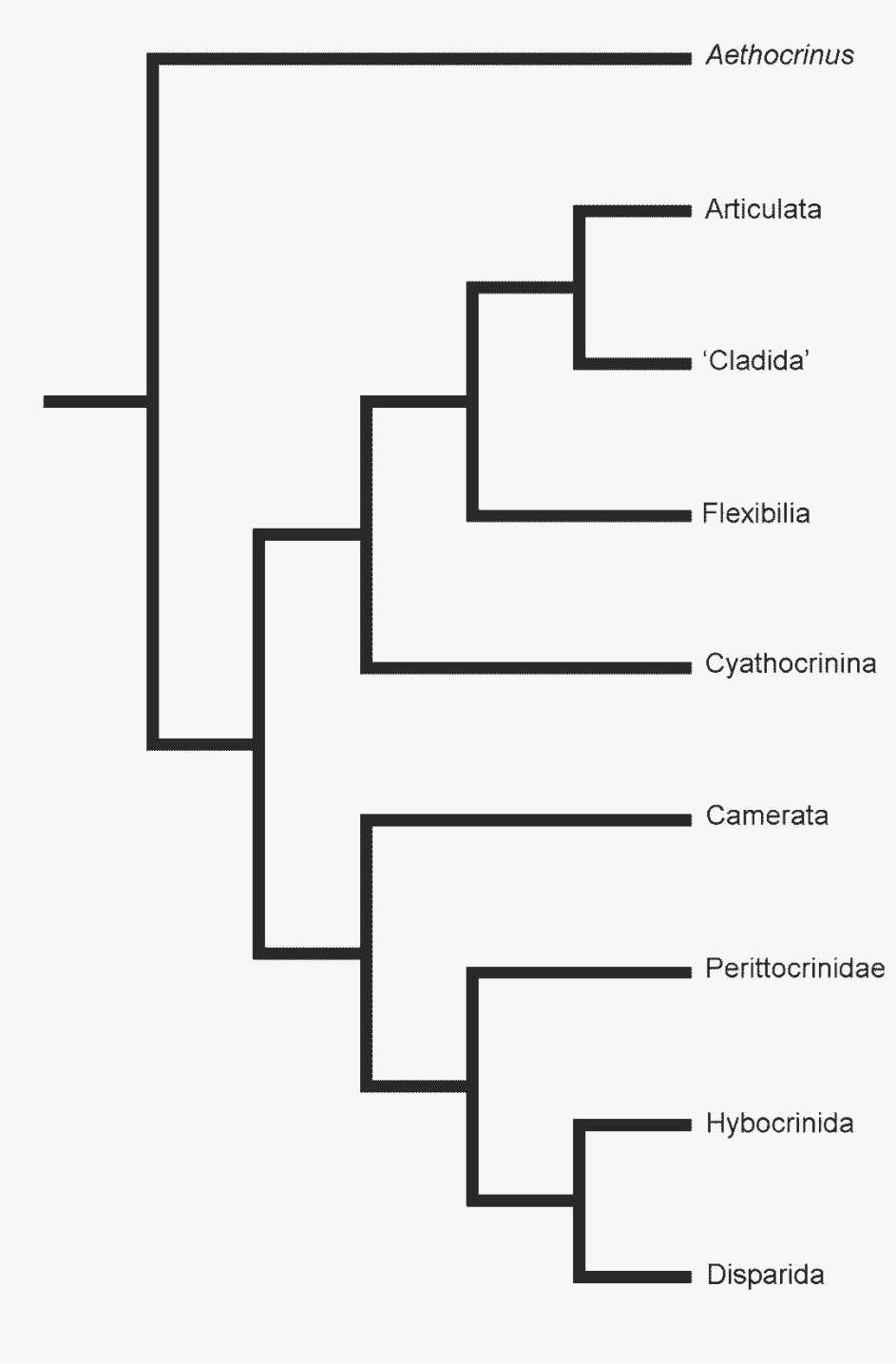

Figure 2.4: Cladogram obtained through analysis conducted by Simms, 1994. *Aethocrinus* was chosen as the outgroup (Modified from Simms, 1994).

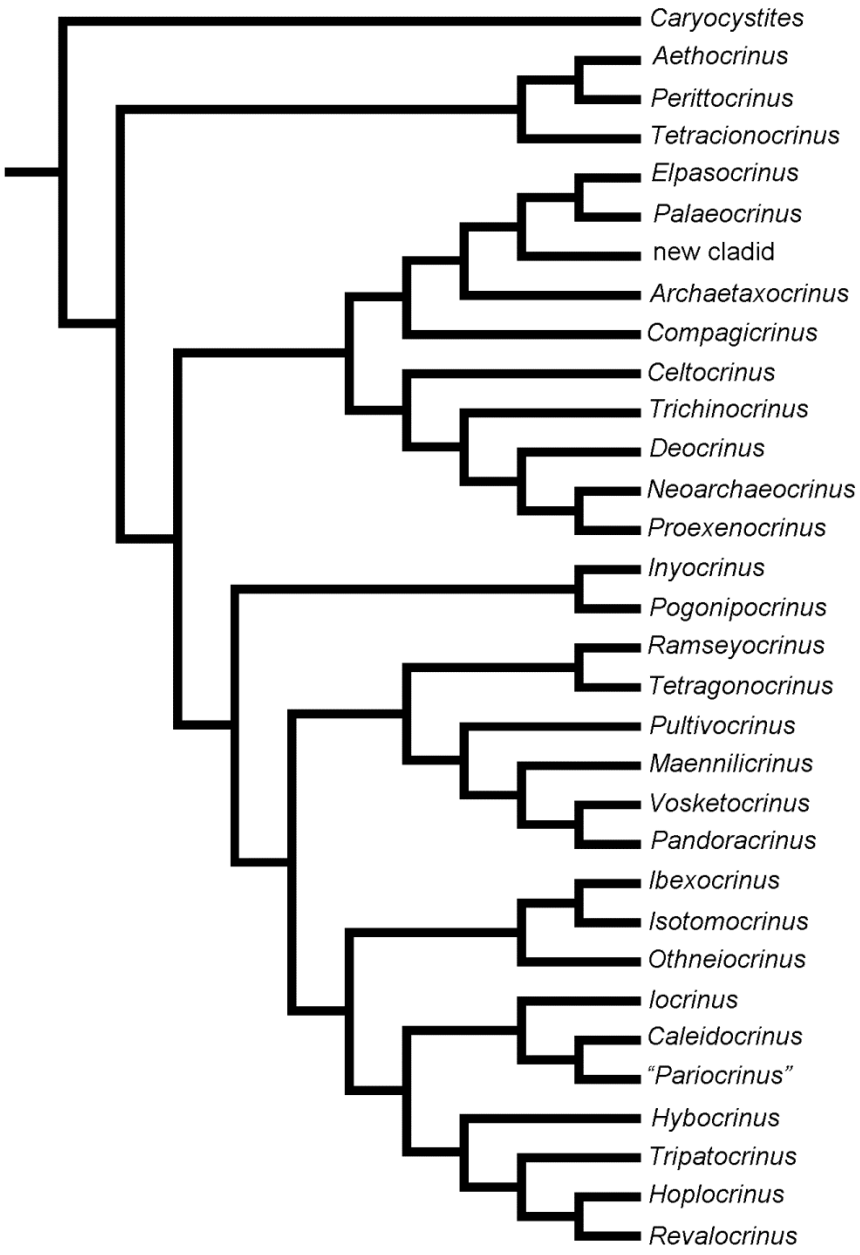

Figure 2.5: Cladogram obtained through analysis conducted by Ausich, 1998. *Caryocystites* was chosen as the outgroup. Tree represents a 50% majority rule of 44 most parsimonious trees, CI= 0.52 (modified from Ausich, 1998).

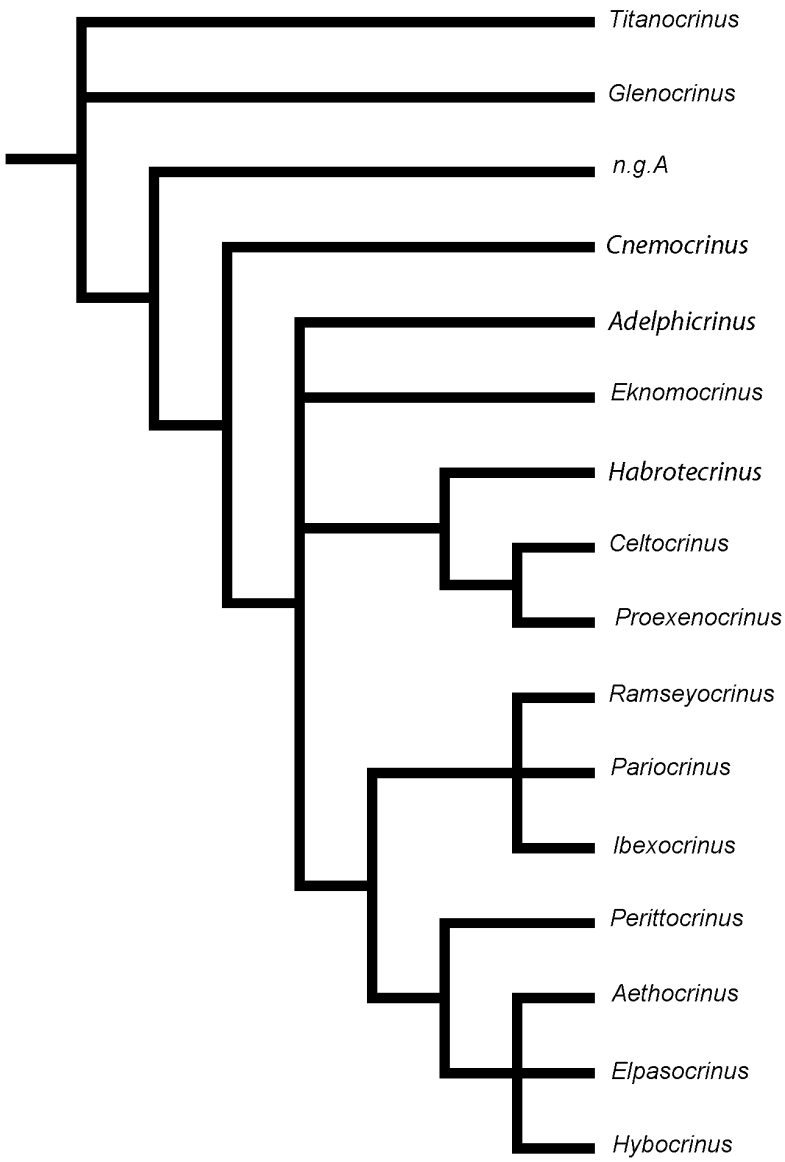

Figure 2.6: Cladogram obtained through analysis conducted by Guensburg & Sprinkle, 2003. Protocrinids were chosen as the outgroup (modified from Guensburg & Sprinkle, 2003)

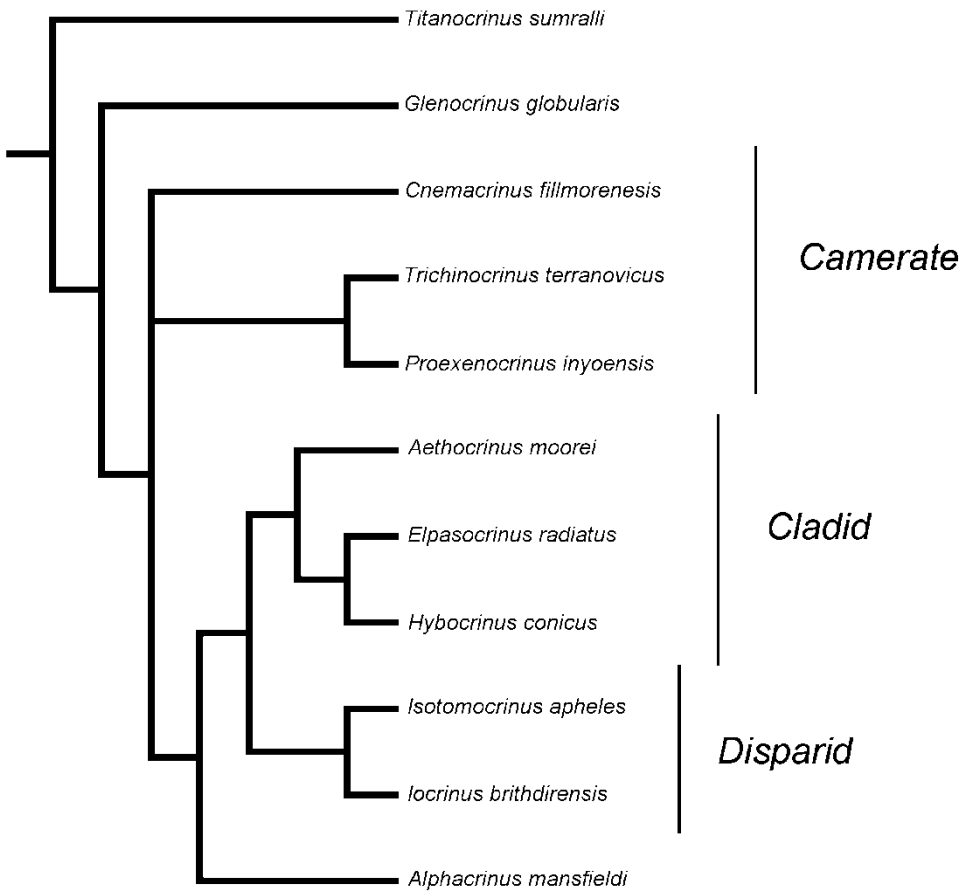

Figure 2.7: Strict consensus cladogram obtained from current analysis. 11 taxa are present, with protocrinids acting as the outgroup. 16 characters were used, and a heuristic search resulted in four most parsimonious trees. Treelength is 36, CI=0.765, RI=0.784, CR=0.599.

Chapter 3: *Biogeography and dispersal of crinoids in the Ordovician*

BIAS IN THE FOSSIL RECORD

The fossil record is the only direct evidence of the history of life on Earth. However, the fossil record is far from complete. This notion has been present in the field of paleontology for well over a century. So evident is the incompleteness of the fossil record that Darwin emphasized it in *On the Origin of Species*. Many people to this day claim the fossil record is spotty and lacks transitional fossils. However incomplete it may be, the fossil record gives researchers a view into the history of life stretching back billions of years.

Burial is the first and most important step toward becoming a fossil. Organisms are more likely to get buried in environments experiencing active deposition compared to those experiencing erosion. This creates a bias in the fossil record toward organisms living in depositional areas. Shallow-water sediments of epicontinental seas and continental shelves contain a majority of marine fossils, which in turn comprise a majority of the known fossil record. Though epicontinental seas only cover about 16% of continents today, in the Paleozoic these seas covered as much as 50% of continents (Valentine, 2004).

The presence of hard structures, a calcium carbonate test, woody xylem, or a chitinous exoskeleton, greatly increases the chances of an organism getting fossilized. Mode of preservation varies depending on composition of the structure. Permineralization, recrystallization, or replacement are common modes of preservation for such structures.

There is also a time bias in the fossil record. This should not be confused with a completeness of the sedimentary sections, which is independent of age. A

stratigraphic section of Cambrian rock should show a level of completeness similar to a section from the Jurassic (Valentine, 2004,). However, the number of exposed sections from different ages will vary, based on younger rocks overlying older ones, erosion of older rock exposed for extended periods of time, tectonic movement, and interactions between plates. The fossil record of deep marine organisms in the Paleozoic is poorly known because only a small amount of oceanic rock has become incorporated into mountain belts on continental plates. Oceanic crust is constantly recycled through the process of subduction. The active subduction of plates means today there is no oceanic crust older than 170 Ma in deep oceans (Lees et al. 2002).

A third bias in the fossil record is a product of population size. Predators are less likely to be preserved than their prey because of their smaller numbers. By this it is meant that the population of a predator, say a fox, is understandably smaller than that of its prey, in this instance rabbits. The presence of more individuals increases the odds of one or more being preserved. Also, localized species with small populations are less often preserved that widespread species with larger populations.

If an organism lived in an environment conducive to burial and gets buried, it then has to survive for a long time. That section of rock must remain free from severe strain or deformation for millions, or even hundreds of millions, of years. Somehow the rock must become exposed at the surface. Rock can become exposed though natural processes such as wind or water erosion, but also though human interactions with the Earth. No matter how formations become exposed, the exposure is never equal over the entire section. Once exposed, there is still a chance that a specimen will not end up as part of the known fossil

record. The reason is the final bias, the collector's bias. Some specimens are never found, and others may be too large to carry out of the field. When conducting field work, scientists do not collect every specimen observed. This is done for various reasons: rocks are heavy; fossils of a given taxon may be overly abundant just to name a few. Also, collectors looking for one taxon in particular might not be interested in collecting another. If specimens are not collected once exposed, weathering processes can cause the fossils to erode and gradually destroyed; similar to the rock it is contained within.

A combination of these biases will affect any paleontological inquiry to some degree. A lack of completeness should not deter researchers, for all science is based on incomplete knowledge (Paul, 1992). However, it is important for researchers to understand how different biases can distort results leading to misinformation.

Understanding how different biases affect ones sample can help to remove uncertainty about incomplete data. For the study of Ordovician crinoids, a number of biases are relevant study. Some biases work in favor of preserving crinoids, whereas other biases will work against preservation. Crinoids, typically inhabiting shallow sea floors during much of the Paleozoic, are found in areas of active deposition. In fact, the fossil record is heavily biased toward marine organisms (Kidwell & Holland, 2002) because of active deposition occurring in shallow oceans alongside continents.

Crinoids possess a rigid calcareous internal test composed of numerous individual plates. The presence of such a skeletal structure increases the chances of a crinoid becoming part of the fossil record compared to many other invertebrates. A majority of the plates are connected with ligamentary

articulations (see section on crinoid morphology for more detail), and because crinoids rely on ocean currents for feeding, the same energy that brings food during life can result in disarticulation after death. For example, almost no taxa observed from the Early Ordovician have been discovered in their complete form (arms, calyx, column, and holdfast intact).

Time is the most important bias acting upon the organisms investigated herein, for it is time that will allow many of the other biases to affect specimens. Over 450 million years of tectonic activity, erosion, and deposition has likely exposed, distorted, or destroyed many fossil crinoids. What is left is only a handful of taxa from the Early to Middle Ordovician. Such small sample sizes, some taxa represented only by two or three partially preserved specimens, could yield what will eventually become incorrect information about the early radiation and distribution of crinoids.

Paleogeography and a geographic collection bias can also skew results of such studies. Ordovician rocks from North America and Europe were located equatorially for much of the Paleozoic. High sea levels during much of this time resulted in large epicontinental oceans. Marine organisms, and specifically crinoids, show a strong collection bias toward North America and Europe (Kidwell & Holland, 2002). Observation of radiation patterns based on incomplete geographic sampling should be biased toward those countries. Trends observed with current data may become obsolete as researchers begin to explore exposures of Ordovician rocks located on the continents that composed Gondwana in the Early Paleozoic (Sumrall and Zamora, 2011).

Population size could be affecting sampling, although the extent of this bias is difficult to quantify for the samples of interest here. Before undergoing a

major radiation in the Middle to Late Ordovician, crinoids may have been relatively rare. Alternatively, the small sample sizes could result from a combination of biases affecting preservation.

The collector's bias generally does not affect the study of crinoids in the Ordovician. Most marine invertebrates from this time period are small in size, allowing collectors to gather a number of specimens without creating an overburdened load. Also, echinoderms are typically less abundant than many other phyla and rarity often results in interest. One point where a bias may arise from a collector is not in the field, but in the lab. Once prepared and described, researchers must either identify to which current taxon this sample fits, or create a new taxon to contain the specimen. Often the assignment of different taxa will change through time, as new understandings of relationships arise. For example, one can read three different papers describing the plating in the early crinoid *Aethocrinus moorei*. Each paper will present different names for the differing circlets of plates in the aboral cup (see Ubaghs, 1969; Philip & Strimple, 1971; Ausich, 2004). Further, this specimen is classified into two different subgroups, the Aethocrinids or the Cladids, depending on whose description is read (see Ubaghs, 1969; Ausich, 2004).

In summary, the fossil record is incomplete for a variety of reasons. Environmental conditions, population size, and body composition are all factors affecting initial burial. Taphonomic processes occur over millions of years and can result in varying qualities of preservation. While these processes are occurring, the rock containing the fossil cannot undergo tectonic and metamorphic events that can distort or destroy the fossil. Once fossilized, the specimen must eventually become exposed at the surface, preferably *in situ*

rather than being found later as float. Finally, a collector must pick up the specimen, prepare and describe it, and finally deposit it in a university or museum collection. A persistent effort by researchers continues to yield new taxa from new strata, slowly adding to our knowledge of the history and evolution of life on Earth.

THE ORDOVICIAN PERIOD

The Ordovician Period is the second of the Paleozoic Era. The Paleozoic Era is roughly 300 million years in length, comprising nearly half of the Phanerozoic Eon. Preceding the Ordovician Period is the Cambrian. The Cambrian Period saw a fairly rapid and major increase in the diversity of life, the "Cambrian explosion", with almost all known phyla making their first appearance in the fossil record. The Ordovician Period is currently identified to begin 488.3 million years ago (Ogg et al., 2008). The base of the Ordovician is defined by the lowest occurrence of the conodont *Iapetognathus fluctivagus*, just above the base of the *Cordylodus lindstromi* conodont biozone within bed 23 of the Green Point Formation at Green Point, western Newfoundland, Canada (Cocks et al, 2010). The Ordovician is divided into seven stages, which can be grouped into Early, Middle, and Late ages (Figure 3.1). The Ordovician-Silurian boundary reference section is located at Dob's Linn in Scotland. The boundary is identified by the presence of the graptolite *Glyptograptus persculptus*, near the base of the Birkhill Shale Formation (Cocks et al, 2010).

Paleozoic sea level reconstructions have been created using sequence-stratigraphy and biochronostratigraphy. The study of the Paleozoic is hampered by subduction of oceanic crust, and the abundance of epi- and pericratonic

basins (Haq, 2008). Ice-volume proxies (see Raymo et al., 2006) are also not useful in the Paleozoic because of diagenetic alterations of oxygen isotopes (Haq, 2008). Current models of Early Paleozoic sea level (Figure 3.2) show a sea-level rise from the Cambrian to Early Ordovician, a small drop in the Middle Ordovician, followed by a rise to the highest sea levels observed in the Paleozoic, almost 200 meters above present day (Haq, 2008). The atmospheric conditions during the Ordovician were very different than today. The level of atmospheric CO_2 is the highest seen in the Phanerozoic, roughly fifteen times the level observed today (Berner & Kothavala, 2001).

The Hirnantian glaciation occurring at the end of the Late Ordovician is accepted as the cause of the end-Ordovician extinction, the first of five mass extinctions observed in the Phanerozoic (Sheehan, 2001). Estimates have shown that up to 85% of all species became extinct (Jablonski, 1991). Preceding this mass extinction was a massive radiation and diversification of marine life, the Great Ordovician Biodiversification Event (GOBE). The GOBE gave rise to the Paleozoic Evolutionary Fauna (PEF), a group of organisms that rose to dominate the Paleozoic seas. The rise of the PEF resulted in a tripling of marine diversity (at the Family level), and has been tied to an improved utilization of ecospace (Bambach, 1983). Ecospace parameters include mode of life and feeding type. Mode of life can be pelagic (living in the water column), epifaunal (living on substrate), or infaunal (living within substrate). An epifaunal mode of life can further be broken down into mobile, attached erect, and reclining. The infaunal can be subdivided into shallow and deep modes, and further subdivided into passive and active forms (Bambach, 1983).

In total, three EFs have been described, The Cambrian (CEF), Paleozoic (PEF), and Modern Evolutionary Faunas (MEF) (Figure 3.3). The CEF is characterized by low diversity communities, few suspension feeders, little planktonic food, and simple food webs. The PEF increased the number of epifaunal suspension feeders, planktonic food became more abundant, animals began to move into the water column, and food webs increased in complexity. The MEF is characterized by high diversity communities, epi- and infaunal suspension feeders, an increase in animals inhabiting the water column, and even more complex food webs (Sheehan, 1996).

ORDOVICIAN TECTONICS

The Ordovician Period experienced the greatest continental dispersal of the Paleozoic. Models have shown that geologic intervals with supercontinents tend to show a decreased marine diversity, whereas dispersed continents correlate with an increase in marine diversity (Servais, 2009), which likely helped spur the GOBE. The position of continental plates for most of the Paleozoic represents a configuration between two supercontinents, Rodinia (breaking up around 750 Ma) and Pangea (forming about 250 Ma). The position of continental plates by the Early Ordovician created the largest tropical shelves seen in the Earth's history (Walker et al. 2002).

During much of the Paleozoic, four major continents were present on Earth: Gondwana, Laurentia, Baltica, and Siberia. Towards the end of the Cambrian Period (Figure 3.4), Gondwana stretched from the South Pole to the Equator. It was composed of Central to South America, Africa, the Middle East, Southeast Asia, and Australia. Laurentia (composed of much of North America

and Greenland, also including Scotland and Ireland) was situated at low latitudes, separated from northwest Gondwana (South America) by the Iapetus Ocean. Laurentia would continue to maintain a roughly equatorial position until the end of the Silurian. At this time Baltica was inverted 180 degrees geographically, with its current northeast end faced northwest Gondwana. The margin facing Laurentia is proposed to be a passive one, but active subduction is proposed to be occurring along the opposite coast (Cocks et al, 2002). Siberia was positioned in a subtropical location just south of the Equator.

From the Tremadoc to Late Floian Stage (roughly 490-471 Ma) (Figure 3.5), the Iapetus Ocean was spreading, the distance between Scotland (at the southern tip of Laurentia) and England (on Avalonia though not free from Gondwana yet) is estimated to be about 5000 km. At this time Baltica and Gondwana began drifting apart, expanding the Tornquist Ocean to a width of approximately 1300 km. As Baltica began to diverge from Gondwana, the plate also began to rotate in a counter-clockwise direction (Cocks et al., 2002). Siberia drifted toward the equator, though at a slower rate relative to Baltica (Torsvik et al., 1996). During this time, the Avalonia terrane (containing England) was part of the northwest margin of Gondwana.

As the Dapingian progressed into the Darriwilian and Sandbian Stages (~471-449 Ma) (Figure 3.6), many small terranes began moving away from Gondwana. Avalonia rifted off sometime in the Early Darriwilian. By the Sandbian Avalonia had reached paleolatitudes roughly equal to Baltica, and in the process formed the Rheic Ocean between itself and Gondwana. At the same time a spreading center began to form, pushing southern China, Annamia, and Sibumasu away from Gondwana. The Iapetus Ocean began to close at this time,

the distance between modern-day Avalonia (England) and southern Laurentia (Scotland) becoming reduced to 2000 km.

From the Katian Stage well into the Silurian Period, spreading continued in most areas. The Rheic Ocean between Avalonia and Gondwana continued to widen, reaching a width of roughly 5000 km by the end of the Ordovician. Southern China, Annamia, and Sibumasu all continued to drift away from Gondwana during this time as well. Meanwhile, Avalonia continued its movement north, eventually colliding with Baltica and closing the Tornquist Ocean. Evidence of this collision is observed in paleomagnetic data, along with tectonic and isotope data (Cocks et al., 2002). As these two terranes became one, they continued their movement north, causing the Iapetus Ocean to subduct under the Laurentian plate. During the Late Ordovician Siberia continued slow movement northward, eventually colliding with Baltica and the Kazakh regions in the late Carboniferous (Cocks et al., 2002).

LARVAL BEHAVIOR AND CRINOID DISTRIBUTION

Interpreting dispersal and distribution patterns for extinct organisms can quickly become a complex task. Crinoids exemplify this complexity well. For the present study, the crinoid taxa we can observe today are highly modified from their Paleozoic relatives and are proposed to represent a single lineage that survived the end-Permian extinction. It is unknown to what degree different clades of Paleozoic crinoids were able to disperse. To investigate this complex problem, recent studies of marine larval distribution are used as proxies for this study.

The idea that planktonic larvae can be transported over great distances has been accepted for a number of years (Robertson, 1964), and laboratory studies have shown that echinoderm larvae can delay metamorphosis for extended periods of time (Strathmann, 1978). Two principal methods have been proposed for moving across vast expanses of deep ocean, rafting (attaching to driftwood or kelp wracks) and transportation on ocean currents (Scheltema, 1981).

Focusing on dispersal through oceans by currents, three factors determine the success of drifting. Currents in the area inhabited by the parent population must be conducive to get larvae into ocean currents. Studies of reef-fish larvae have shown that the larvae can be caught in quasigeostrophic eddies (Robinson, 1983). Eddies of this type are seasonal. This means timing of reproduction can be an important factor in determining if larvae are carried away from or kept near the parent population. Larval mortality while in the open ocean will affect the number of larvae available to be transported to another locality. Studies attempting to quantify mortality are very few. Finally, if some larvae do make it to a new suitable habitat, the new population must survive and reproduce (Scheltema, 1986). The aforementioned factors decrease the likelihood of organisms rapidly being distributed over great distances. It is important, however, to remember that when invertebrates undergo spawning they sometimes produce thousands to hundreds of thousands of larvae. Studies have shown a single holothurian is capable of producing hundreds of eggs in a single spawn (McEuen, 1988). Spawning tends to occur at the same time in populations, increasing the number of fertilized larvae into the millions.

Studies of faunal migration around the Iapetus Ocean show that in the latest Cambrian the ocean was wide enough to separate faunal assemblages. Pelagic graptolites are the first organisms to appear on both sides of the ocean, with *Dictyonema flabelliforme* migrating across in the Tremadoc. By the Arenig, many types of graptolites were present on both sides of the ocean. Next to cross the Iapetus Ocean were taxa with a pelagic larval stage, trilobites and brachiopods specifically appearing by the Middle Ordovician. By the end of the Ordovician the assemblages have become cosmopolitan, and distinguishing between the two becomes all but impossible (McKerrow, 1976).

Brachiopods, trilobites, and graptolites have all been studied heavily with regards to biogeography, giving some idea of dispersal patterns of marine invertebrates. In the Early Ordovician, pelagic trilobites have distributions that correspond to paleolatitude and paleogeography. The equatorial trilobites are mainly bathyurids. These trilobites are observed on Laurentia and Siberia, Located roughly subtropical are the Ptychopygine/Megalaspid trilobites. These are isolated on Baltica at this time. Located farther south, near the Antarctic continent are the Calymenacean-Dalmanitacean fauna. These have been found around Gondwana (including the Avalonian terrane) (Cocks et al., 2002). By the end of the Ordovician, all plates are located much closer together, and the distribution of faunas is not restricted to respective continents. Based on observations of this nature, we can hypothesize that crinoids in the Early Ordovician should conform to the same paleolatitude and paleogeographical constraints.

Similar observations have been made with respect to brachiopods. Observations of brachiopod populations in the Early Ordovician indicate the

predominance of single-plate endemics. Plate movement through the Ordovician saw a decrease in the width of major oceans between plates, allowing for increased dispersal of organisms (Lees et al. 2002). By the end-Ordovician the predominance of single-plate endemics diminishes substantially (Lees et al. 2002).

CRINOID DISTRIBUTION IN THE PALEOZOIC

Based on work done with other taxa, it is helpful to discuss crinoids of the Ordovician based on “provinces”, areas that are likely isolated reproductively for the period of study. These provinces are based on geographical position and latitudinal variation. Key faunal provinces are the Northern Laurentian province, Southern Laurentian province, Avalonian province, Gondwana province, and Baltica province.

Possible ancestral locations for crinoids were gathered using the strict consensus cladogram obtained in chapter two. No taxa from the Baltica were present in the cladistics analysis. Mapping character history over the cladogram indicates a Northern Laurentian origin for crinoids (Figure 3.7). Locality datum for the taxa of interest were collected and plotted on paleogeograhic maps with plate locations corresponding to the Tremadocian (Figure 3.8) and Floian (figure 3.9) stages. No taxa used in the cladistic analysis were present in the Dariwillian. These figures illustrate the locality of the earliest known crinoids and give a visual representation of what is seen in Figure 3.7.

Now that an ancestral area has been defined, dispersal trends can be further elucidated by including more taxa. The cladogram from chapter two retained three monophyletic groupings that are in alignment with the classic

groupings used by researchers for decades. Assuming that many classically described dispards would group with disparids on the cladogram, and the same would be true of the camerates and cladids, we can look for bigger trends in dispersal.

Locality data for all known crinoids from the Early Ordovician and a large sample of Middle Ordovician taxa was collected and plotted on paleogeographic maps (Table 3.1) Taxa used are placed in one of the three clades observed in the previous analysis based on similarities to studied taxa. While recently described taxa contain detailed descriptions of the locality, locality information from taxa discovered in the late 1800's and early 1900's is imprecise at best and at worst lacking altogether. However, every attempt was made to identify as precisely as possible all localities. Data was entered at the University of Texas Institute for Geophysics (UTIG). With the help of the PLATES Project, all data were plotted on plate reconstructions for the appropriate Ordovician age. Reconstructions were obtained for 483, 475, and 465 Ma (Lawver et al, 2010). Dates of map reconstructions are plotted on Figure 3.1.

The earliest known crinoids come from the Tremadocian. Plate reconstructions from the middle Tremadoc Stage show the dispersal of all known taxa from this stage (~483 Ma) (Figure 3.8). The Northern Laurnetian province has all morphological groups present, including taxa identified as disparids, cladids, camerates, and protocrinids. In the Southern Laurentian province camerate and disparid stocks are present. At this time the Baltica and Avalonian provinces lack any crinoid specimens. The Avalonian province contains a single specimen with disparid affinities. Though weakly supported with so few taxa, these data paint a picture of disparid-like taxa being most widely dispersed even

in the Earliest Ordovician, whereas taxa with Camerate affinities are isolated to the Laurentian provinces. Of all taxa present in this time slice, the protocrinids are the only stock that does not advance beyond the Tremadocian Stage.

The next time slice observed occurs in the late Early Ordovician, corresponding to the middle of the Floian Stage (~475 Ma) (Figure 3.10). At this time the Northern Laurentian province has extended its range south to include present day central U.S.A. The camerate, cladid, and disparid stocks are still present. One taxon with cladid affinities, *Aethocrinus moorei*, appears in a strange location. These reconstructions show the locality being far south on Gondwana. However, other researchers have suggested this specimen may be located on the northeastern margin of Gondwana and much further north. The original publication indicates a large amount of uncertainty as to the exact horizon from which these specimens came from because the fossils were discovered as float, rather than *in situ*. The region in southern France where this specimen was discovered is tectonically complex, further compounding the issue.

By the second half of the Middle Ordovician (~465 Ma) (Figure 3.11), taxa with camerate affinities have expanded their range to the Avalonian province, but have not yet become a part of the Baltica province. The Baltica province at this point in time is solely composed of disparid stock. The Northern Laurentian province continues to show the most diversity, with cladids and disparids still present. In this time slice, two taxa from the disparid stock appear very far south on Gondwana. These specimens were, like the previous problematic taxon, located in southern France. The description of these taxa appears to be lacking in specific locality information other than the name of the nearest city.

DISCUSSION

Biogeographical studies have supported diversity and radiation patterns for several different marine organisms in the Ordovician. Trilobites and brachiopods are confined to individual plates in the Early Ordovician, but by the end of the period many populations have become cosmopolitan. A similar trend is observed for all crinoids, except the disparid clade. This difference in distribution for disparids could be an artifact of the fossil record bias. Thirty taxa were observed for this study, of which sixteen are identified as disparids, with the remaining divided between the four other morphological groups.

Analysis at the Linnaean family level shows, even with an interesting dispersal of disparids early on, closely related taxa tend to group together geographically. Iocrinids appear first in the Avalonian province, and eventually cross the Tornquist Ocean to inhabit the Baltica province during the Early Ordovician. Eustenocrinids are isolated on the Laurentian platform (Northern Laurentian province) for the first half of the Early Ordovician, extending their range to the Baltica province by the end of the Early Ordovician.

Camerate-like crinoids are isolated on Laurentia until the late Early Ordovician (Floian). On Laurentia, members of the family Rhodocrinitidae are present in both the Northern and Southern Laurentian provoinces, indicating the possibility that what was previously proposed to be two faunal provinces could possibly be a single province. By the late middle Ordovician camerate crinoids had crossed the Iapetus Ocean from Laurentia and extended their range to Avalonia. One taxon is present in Avalonia at this time, but identification at the family level is uncertain because of poor preservation and weathering of the specimen.

Observations of the cladid stock indicate this group was also radiating from the Laurentian platform. By the end of the Early Ordovician cladids are known from the Northern and Southern Laurentian provinces, but through the Middle Ordovician this group seems to remain isolated on Laurentia. Uncertainty about family level identification and poorly documented locality information makes any certain diagnosis impossible, but the first appearance of this group indicates origins similar to those seen in the camerates. Protocrinids are restricted to the first half of the Early Ordovician. This group possesses many characteristics similar to those observed in the camerate stock, and could be ancestral to the camerates.

CONCLUSIONS

The origin and relationship of the major groups of crinoids have been studied for over a century. Even with such a long history of research, these relationships are not well understood. Crinoids definitively appear in the fossil record in the Early Ordovician. Even in the earliest Ordovician crinoids are divisible into three or four morphological stocks. If crinoids are in fact a monophyletic clade, a divergence must have occurred sometime in the Cambrian. A specimen from the Burgess Shale, *Echmatocrinus brachiatus*, was originally diagnosed as the earliest crinoid (Sprinkle, 1973), though this diagnosis has been recently challenged (see Ausich & Babcock, 1996, 1998; also Sprinkle & Collins, 1995, 1998). If this specimen is interpreted as a basal echinoderm, it may help to explain the appearance and radiation of crinoids on Laurentia, but it does not help to explain the presence of widespread disparid taxa by the Early Ordovician.

The dispersal of disparid stock in the Early Ordovician does not show the latitudinal constraints observed in other marine phyla. This taxon being present in all faunal provinces can be explained by two differing hypotheses. First, the larvae of Paleozoic crinoids may be more mobile than what is observed today, possibly also possessing the ability to retain a pelagic larval form for extended periods of time. The second hypothesis would involve the disparid stock dispersing at a point when Baltica and Laurentia were still near one another after the break-up of Rodinia. This hypothesis pushes the origin of crinoids into the Early Cambrian, a very unlikely situation based on what the fossil record has produced so far.

Other crinoid groups, the camerates and cladids, show a pattern more in line with that observed in other phyla. Camerates appear on the Laurentian platform in the Early Ordovician, and extend their biogeographic range to Avalonia by the end of the Early Ordovician. By the Late Ordovician the camerate stock is observed in all faunal provinces. A similar trend is observed for the cladids; which also appear first on the Laurentian platform, although during the first half of the Ordovician these taxa appear to be restricted to the tropical waters surrounding Laurentia. Hybocrinids, proposed by some researchers to be evolutionary descendants of the disparid stock (Ausich, 1996) and by other workers to be cladids with reduced cup plating (Sprinkle, 1981), show a radiation pattern similar to disparids. These observed trends are supported by analysis indicating an likely Laurentian origin for crinoids.

By the Late Ordovician, crinoids had undergone a massive biodiversification (Sprinkle and Guensburg, 2003). In the Late Ordovician plate movement placed the previously discussed faunal provinces in a close enough

proximity to allow larval dispersal between them. This resulted in a largely cosmopolitan crinoid distribution pattern leading up to the Hirnantian glaciation.

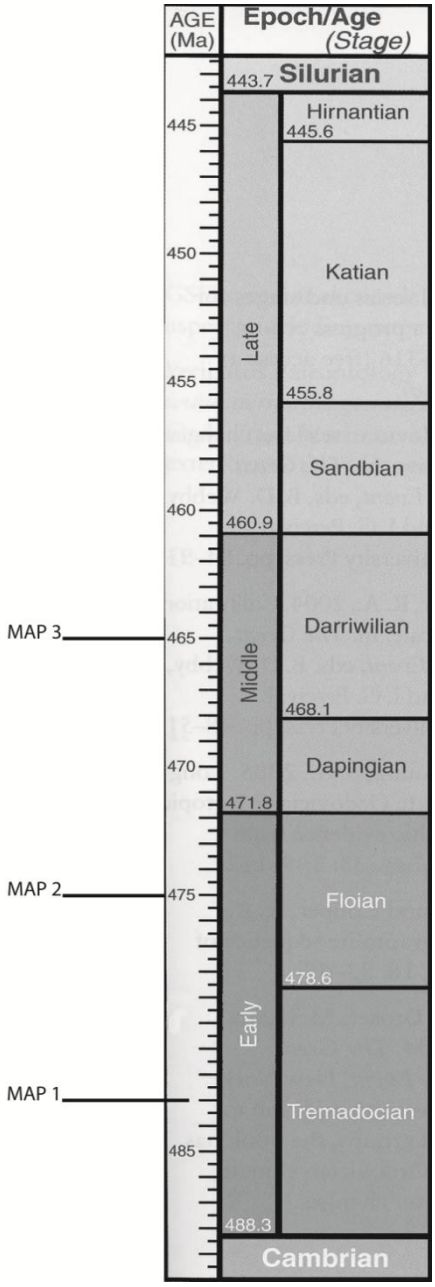

Figure 3.1: Ordovician Period Timescale (modified from Ogg et al., 2008 (MAP 1 corresponds to Figure 3.8, MAP 2 to Figures 3.9 and 3.10, MAP 3 to Figure 3.11).

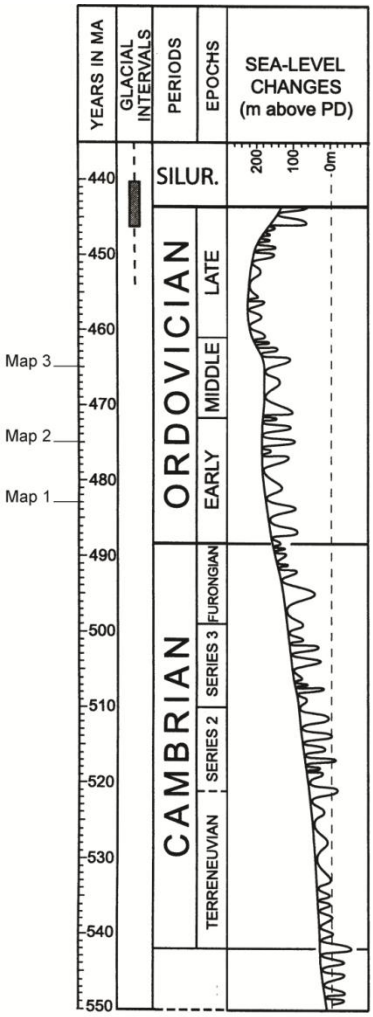

Figure 3.2: Sea-level curve for the Early Paleozoic (Cambrian and Ordovician Periods) showing both short-term (third-order) and long-term fluctuations. Dashed vertical line indicates present day sea level (modified from Haq and Schutter, 2008) (MAP 1 corresponds to Figure 3.8, MAP 2 to Figures 3.9 and 3.10, MAP 3 to Figure 3.11).

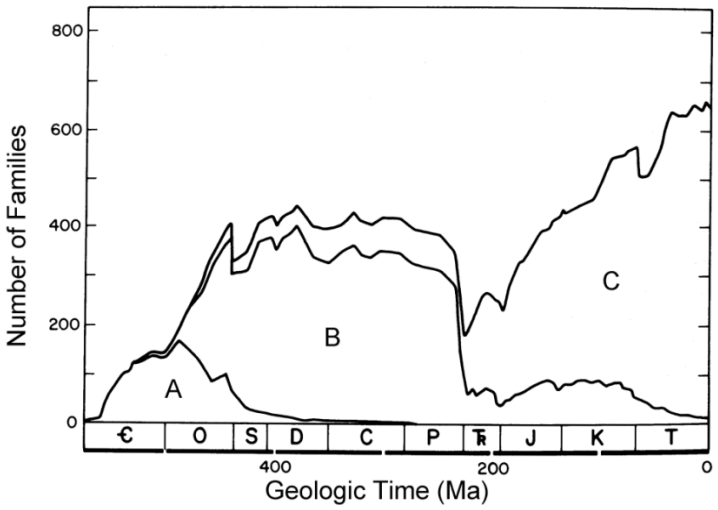

Figure 3.3: Diversity of marine taxa (at Family level) through the Phanerozoic (modified from Sepkoski, 1981). (A) Cambrian Evolutionary Fauna, (B) Paleozoic Evolutionary Fauna, (C) Modern Evolutionary Fauna.

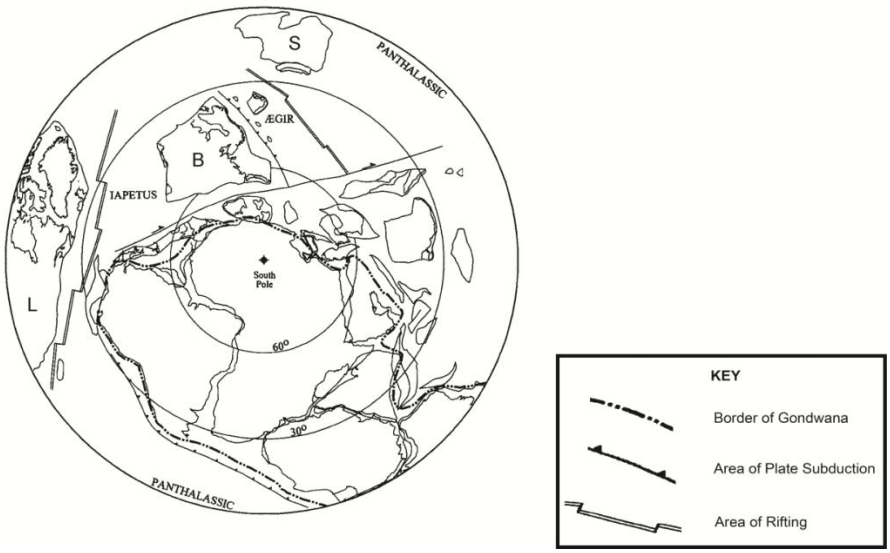

Figure 3.4: Plate reconstruction for the Late Cambrian (~500Ma). Schmidt's Equal Area projection, with projection center at the South Pole (modified from Cocks et al., 2002). L=Laurentia, B=Baltica, S=Siberia.

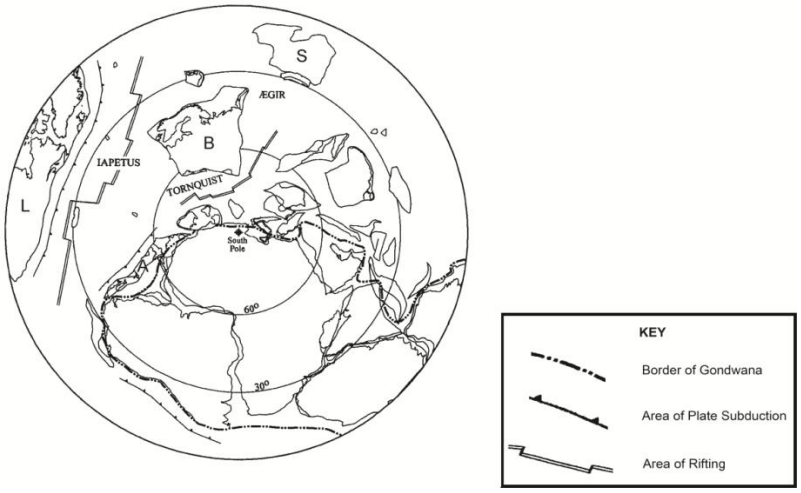

Figure 3.5: Plate reconstruction for the Early Ordovician (~480Ma). Schmidt's Equal Area projection, with projection center at the South Pole (modified from Cocks et al., 2002). L=Laurentia, B=Baltica, S=Siberia, A=Avalonia.

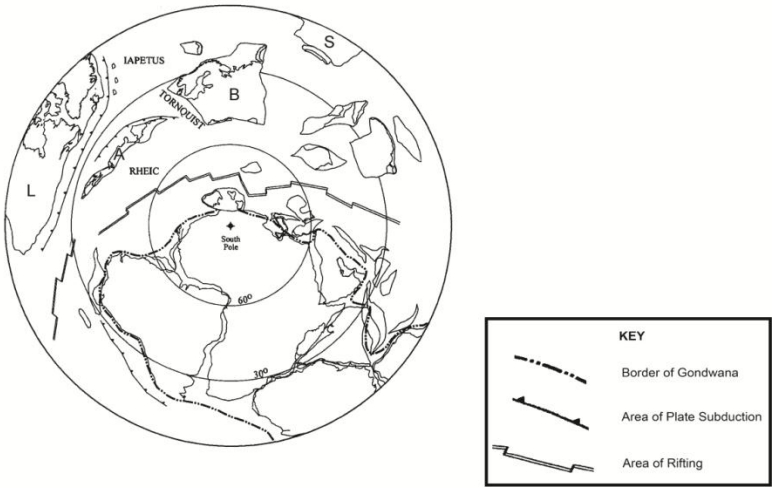

Figure 3.6: Plate reconstruction for the Late Ordovician (~460Ma). Schmidt's Equal Area projection, with projection center at the South Pole (modified from Cocks et al., 2002). L=Laurentia, B=Baltica, S=Siberia, A=Avalonia.

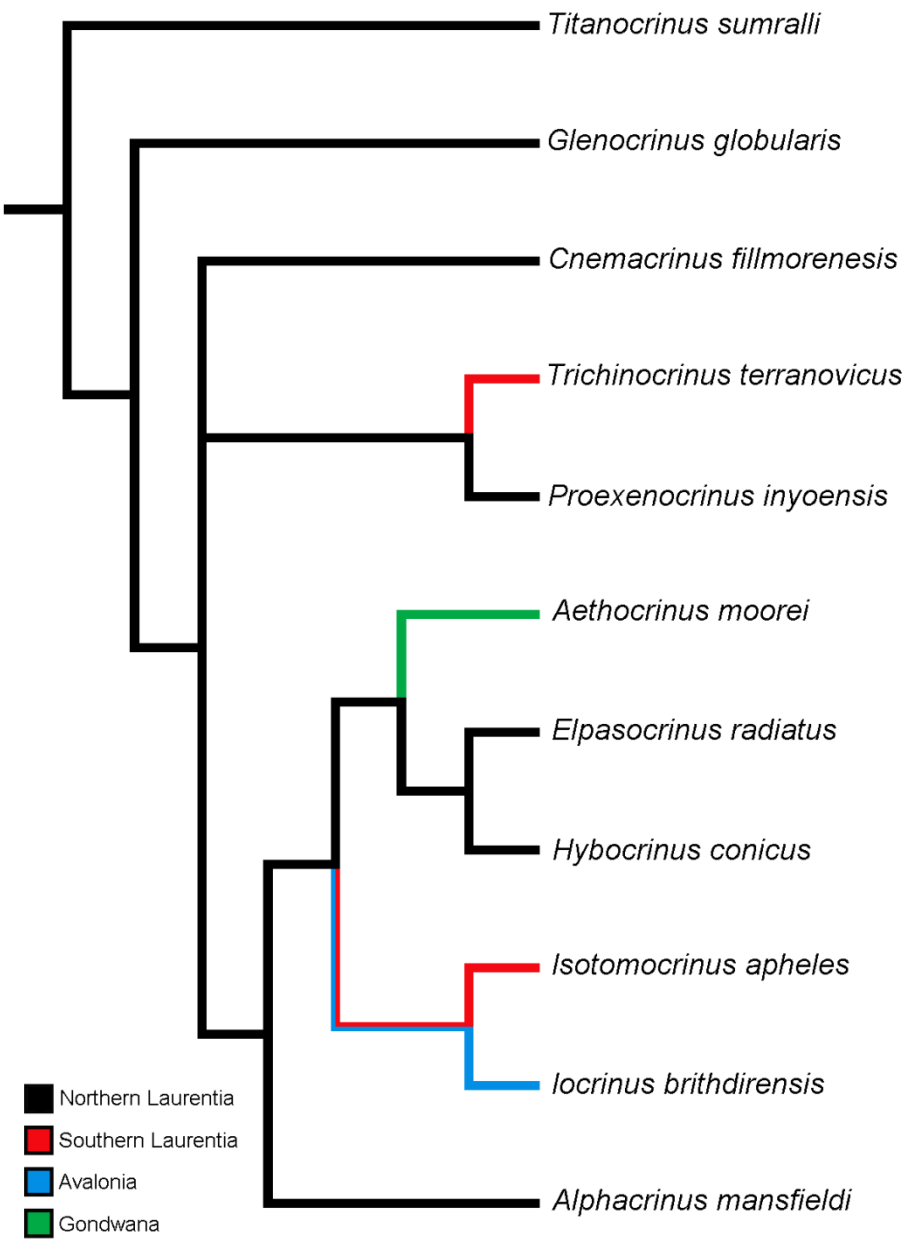

Figure 3.7: Cladogram with biogeographic location mapped on tree (parsimony reconstruction).

Figure 3.8: Plate reconstruction for the Middle Tremadocian (~483 Ma) with cladistics analysis taxa present. Azimuthal projection centered at 70°W, 20°S. Map data provided by the UTIG PLATES Project. Symbols represent taxa from Table 3.1.

Figure 3.9: Plate reconstruction for the Middle Floian (~475 Ma) with cladistics analysis taxa present. Azimuthal projection centered at 70°W, 20°S. Map data provided by the UTIG PLATES Project. Symbols represent taxa from Table 3.1.

Figure 3.10: Plate reconstruction for the Middle Floian (~475 Ma) with other crnoid taxa present. Azimuthal projection centered at 70°W, 20°S. Map data provided by the UTIG PLATES Project. Symbols represent taxa from Table 3.1.

Figure 3.11: Plate reconstruction for the Middle Darriwilian (~465 Ma) with other taxa present. Azimuthal projection centered at 70°W, 20°S. Map data provided by the UTIG PLATES Project. Symbols represent taxa from Table 3.1.

Taxon	Family Classification	LAT	LONG	Map ID
Titanocrinus sumralli	Titanocrinidae	39.0612°	-113.1918°	**P1**
Glenocrinus globularis	Titanocrinidae	39.0612°	-113.1918°	**P2**
Cnemacrinus fillmorensis	Reteocrinidae	39.0612°	-113.1918°	**C1**
Trichinocrinus terranovicus	Rhodocrinitidae	48.5634°	-58.7749°	**C2**
Inyocrinus strimplei	Eustenocrinidae	36.9464°	-118.1021°	**D4**
Alphacrinus mansfieldi	Alphacrinidae	39.0343°	-113.3660°	**CI1**
Iocrinus brithdirensis	Iocrinidae	53.113095°	-4.122050°	**D3**
Isotomocrinus apheles	Cincinnaticrinidae	48.5612°	-58.7389°	**D2**
Apektocrinus ubaghsi	Apektocrinidae	42.0895°	-111.6332°	**CI3**
Proexenocrinus Inyoensis	Rhodocrinitidae	36.9464°	-118.1021°	**C4**
Aethocrinus moorei	Incertae familae	43.445080°	2.334726°	**CI2**
Hybocrinus conicus	Hybocrinidae	43.390349°	-91.818479°	**H1**
Compagicrinus fenestratus	Dendrocrinidae	80.045855°	-65.592752°	**oCI1**
Othneiocrinus priscus	Heterocrinidae	38.8563°	-113.4604°	**oD5**
Ibexocrinus lepton	Homocrinidae	38.8563°	-113.4604°	**oD6**
Pogonipocrinus antiquus	Eustenocrinidae	39.043711°	-113.347903°	**oD8**
Maennilicrinus concinnus	Iocrinidae	59.864998°	31.469407°	**oD9**
"Pariocrinus" ladogensis	Iocrinidae	59.864998°	31.469407°	**oD12**
Archaetaxocrinus burfordi	Taxocrinidae?	34.3686°	-97.1510°	**oCI2**
Tetragonocrinus pygmaeus	Incertae familae	59.2334°	31.4333°	**oD10**
Neoarchaeocrinus pyriformis	Archaeocrinidae	55.171172°	-4.817638°	**oC1**
Celtocrinus ubaghsi	Incertae familae	51.880127°	-4.939864°	**C3**
Elpasocrinus radiatus	Dendrocrinidae	31.7838°	-106.4809°	**CI4**
Hoplocrinus dipentas	Hybocrinidae	36.3868°	-115.6819°	**H2**
Caleidocrinus turgidulus	Iocrinidae	52.186976°	-3.361842°	**oD1**
Pandoracrinus pinnulatus	Botryocrinidae	50.622582°	13.691943°	**oD2**
Vosekocrinus granulatus	Incertae familae	50.622582°	13.691943°	**oD3**
Revalocrinus costatus	Hybocrinidae	59.438862°	24.754472°	**oD4**
Tripatocrinus pustulatus	Cornucrinidae	36.398569°	-115.372635°	**oD7**
Pultivocrinus fundatus	Eustenocrinidae	59.864998°	31.469407°	**oD11**

Table 3.1: Locality data of taxa used in the biogeography study. Map ID refers to data points on Figures 3.8, 9, 10,11, and 12.

Appendix A

1. Aboral cup condition: The arrangement of plates in multiple circlets to form the aboral calyx

States:

0- *Irregular*- multiple plates irregularly arranged in the aboral cup

1- *four-circlet*- four circlets of organized plates in the aboral cup

2- *three-circlet*- three circlets of organized plates in the aboral cup

3- *two-circlet*- two circlets of organized plates in the aboral cup

2. Radial facet: Properties of the structure where the first primibrachial attaches to the radial plate

States:

0- *angustary*- width of primibrach 1 is narrower than the distal margin of the radial plate

1- *peneplenary*- width of primibrach 1 has an equal width with respect to the distal margin of the radial plate

2- *plenary*- width of primibrach 1 is wider than the distal margin of the radial plate

3- *fixed*- primibrach fixed in aboral cup

3. Gap plates: Plates present between the infrabasal plates, typically half the height of infrabasals and not interrupting the circlet

States:

0- *Present*- gap plates present within the infrabasal circlet

1- *Absent*- no gap plates present within the infrabasal circlet

4. Radial Circlet Interruption: Accessory plates that separate the radials

States:

0- *None*- no accessory plates interrupting the radial circlet

1- *In CD interray only*- accessory plates interrupting the radial circlet only in the wider CD interray

2- *In all rays*- accessory plates present between all radials

5. C-radial characteristic: How the C-radial compare in size to all other radials

States:

0- *Same*- C-radial equal in size to all other radials

1- *Smaller*- C-radial smaller than all other radials

6. Proximal Column Type: Construction of the column at the proximal end

States:

0- *Heteromorphic*- column composed of varying columnals termed nodal and internodal. Nodal columnals are added at the stem-cup junction, internodals are added just below and between proximal nodals

1- *Homeomorphic*- all columnal the same size and inserted at the stem-cup junction

7. Proximal Columnal Construction: Construction of columnal near the stem-cup junction

States:

0- *Pentameric*- Each columnal composed of five individual plates

1- *Holomeric*- Each columnal composed of a single plate

8. Proximal Lumen Shape: Shape of lumen in transverse section near the stem-cup junction

States:

0- *Pentalobate*- Lumen pentalobate in transverse section

1- *Pentagonal*- Lumen pentagonal in transverse section

2- *Circular*- Lumen circular in transverse section

9. Fixed Arm Branching: branching pattern of lower arms, whether first axillary plate is incorporated into aboral cup

States:

0- *Present*

1- *Absent*

10. Interbrachial Plates: Accessory plates present between fixed brachials

States:

0 *Present*

1 *Absent*

11. Primary Arm Branching: Arm branching observed in the main arm ray

States:

0- *Isotomous*- Arms branch equally in two directions

1- *Heterotomous*- Arms branch unequally

2- *Atomous*- Arms show no branching

12. Secondary Arm Branching: Arm branching resulting in the presence of specialized feeding structures

States:

0- *Absent*- No specialized feeding appendages present

1- *Isotomous with pinnules*- Isotomous branching of arm rays resulting in the presence of pinnules on each brachial, alternating sides on each respective brachial

2- *Isotomous with endotomous ramules*- Arm rays branch isotomously, with ramules branching off endotomously at regular intervals

13. Highest Fixed Brachial: At what stage in arm branching does the arm become free

States:

0- *Primibrach*- Arms become free on a primibrach

1- *Secundibrach*- Arms become free on a secundbrach

2- *Free on Radials*- Arms are free on radials, no fixed brachials present

14. Number of Arm Bifurcations: The number of times arm rays undergo bifurcation

States:

0- *None*- Arms do not undergo bifurcation

1- *One*- Arms only bifurcate once

2- *Two*- Arms bifurcate twice

3- *Three or more*- Arms bifurcate four or more times

15. Number of primibrachials: Number of brachial plates present after the radial plates and including the first axillary plate

States:

0- *All*- All brachials are primibrachs because the arm is atomous

1- *Five or More*- The first arm bifurcation occurs on or after the fifth primibrachial

2- *Less than Five*- The first arm bifurcations occurs before the fifth primibrachial

16. Brachial plate condition: Shape of brachial plate in aboral view

States:

0- *Rectangular Uniserial*

1- *Cuneate Uniserial*

Appendix B

Character #	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Titanocrinus. sumralli	0	3	0	2	0	0	0	2	0	0	0	0	0	3	0	0
Glenocrinus globularis	0	3	0	2	0	0	0	1	0	0	1	0	0	3	0	0
Cnemacrinus fillmorensis	3	3	1	2	0	0	0	1	0	0	0	0	0	3	0	0
Trichinocrinus terranovicus	3	3	1	1	0	0	?	1	1	0	0	1	1	1	0	1
Proexenocrinus inyoensis	3	3	1	2	0	1	?	?	1	0	0	1	1	2	0	1
Aethocrinus moorei	1	3	1	1	1	0	0	0	0	1	0	0	2	2	1	0
Elpasocrinus radiatus	2	0	1	1	1	0	?	2	1	1	0	0	2	2	1	0
Hybocrinus conicus	2	0	1	0	1	1	?	0	1	1	2	0	2	0	2	0
Isotomocrinus aphales	2	2	1	0	1	0	0	1	0	1	0	0	2	3	1	0
Iocrinus brithdirensis	2	1	1	0	1	0	0	1	0	1	0	0	2	3	1	0
Alphacrinus mansfieldi	2	0	1	1	0	0	0	1	0	1	0	2	0	1	0	0

Character Key (see appendix A for state definitions)

1 Aboral cup position
2 radial facet
3 gap plates
4 Radial circlet interruption
5 C-radial characteristic
6 Proximal column type
7 Proximal column construction
8 Proximal lumen shape
9 Fixed arm branching
10 Interbrachial plates
11 Primary arm branching
12 Secondary arm branching
13 Highest fixed brachial
14 Number of arm bifurcations
15 Number of primibrachials
16 Brachial plate condition

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Vita

Kyle Womack was born in the town of Visalia, located in the Central Valley of California. His passion for marine invertebrates can be traced back to tide pooling with his grandfather around the central coast of California as a young boy. After graduating from high school he earned a Bachelor of Science at the University of the Pacific in Stockton, CA. There he double majored in Biological Sciences and Environmental Studies. It was during this time that he discovered the world of geological sciences through his interest in invertebrate paleontology.

During his time at the Jackson School of Geosciences he was able to interact with a number of amazing people. Besides being a Teaching Assistant in several courses, he volunteered at the Non-vertebrate Paleontology Laboratory, he helped a vertebrate paleontologist in the field, and even employed resources at the University of Texas Institute for Geophysics to complete his thesis. He was also an active member of the Graduate Student Executive Committee, serving as President for one year. This brought him into contact with the Dean, Dean of Students, student advisor, and graduate coordinator to help with many aspects of the Jackson School other than academics and research.

Upon graduation, Kyle moved back to Central California.

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This thesis was typed by the author, Kyle Richard Womack.